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## A REVISION OF THE GENUS SCHKUHRIA

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*Schkuhria* is a member of the tribe Helenieae of the family Compositae. The problem of the correct generic name for this group of plants was considered by a Special Committee for Phanerogamae and Pteridophyta appointed by the 6th International Botanical Congress, Amsterdam, 1935. The action of the committee relegates the *Schkuhria* Moench (1794) to synonymy under *Siegesbeckia*, rejects *Tetracarpum* Moench (1802), and validates *Schkuhria* Roth (1797). The type species is designated as *S. abrotanoides* Roth, Cat. Bot. 1:116. 1797.<sup>2</sup>

Asa Gray was one of the first to make valuable contributions to the knowledge of the genus in his "Notes on Compositae"<sup>3</sup>, and his later revision in "Contributions to North American Botany"<sup>4</sup>. The next extensive revision of the genus was P. A. Rydberg's treatment of the North American species for the North American Flora<sup>5</sup> in which eight species were recognized as belonging to *Tetracarpum*, and a new genus, *Cephalobembix*, was created for *S. multiflora*. The most recent work on the genus is A. L. Cabrera's excellent paper on the Argentine species<sup>6</sup>. All in all, the genus has never been monographed, and since the time of Gray has not been treated in its entirety.

The overlapping of morphological characters makes it difficult to separate several genera in the tribe Helenieae<sup>7</sup>. Nor has it been easy to separate *Schkuhria*

<sup>1</sup> In the fall of 1943 Mr. Norlan C. Henderson, a fellow student in the Henry Shaw School of Botany of Washington University, began a study of *Schkuhria*, but was unable to complete it because of conditions incident to the war. For his use the representation of this genus in the Missouri Botanical Garden Herbarium had been supplemented through loans from several of the larger American herbaria. The assemblage of this relatively large series of specimens afforded an excellent opportunity for a critical study of the group, and with the approval of Mr. Henderson the work was continued. The results are here recorded in the form of a preliminary revision of the genus.

<sup>2</sup> Kew Bull. Misc. Inf., p. 129. 1940.

<sup>3</sup> Gray in Proc. Am. Acad. 9:198. 1874.

<sup>4</sup> *Ibid.* 19:27. 1883.

<sup>5</sup> Rydberg in N. Am. Fl. 34:44. 1914.

<sup>6</sup> Cabrera in Anal. Soc. Cient. Argent. 114:187. 1932.

<sup>7</sup> See Gray, *loc. cit.*, and in Proc. Am. Acad. 15:40. 1879.

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from the closely related genus, *Babia*, although Rydberg<sup>8</sup> places them in different subtribes. The fact that no or only a very few ligules are present in *Schkubria*, whereas they are numerous in *Babia*, is the most reliable though not natural character separating the two genera. When more specimens of *Babia* are available this problem should be examined in greater detail. Although few generic transfers have been made in this paper, future study may warrant them. The "true" *Schkuhrias* are *S. pinnata* (Lam.) O. Kuntze and *S. anthemoidea* (DC.) Coult. and their varieties, while the remaining species of the genus are very closely related to certain species of *Babia*, namely, *B. Bigelovii* Gray, *B. Schaffneri* S. Wats., *B. xylopoda* Greenm., and *B. Pringlei* Greenm.

Within the genus the pappus has always served as the chief diagnostic character, and Gray was one of the earliest to realize that it was "highly probable that the difference in the pappus, although constant in the specimens, is not of specific importance"<sup>9</sup>. However, the pappus, up to the time of Cabrera's<sup>10</sup> work, continued to serve as the main specific character. His realization that the pappus was extremely variable brought about a drastic reduction of the species then recognized in the South American flora. The writer has carried out his principles in the treatment of the North American species. In the present paper a total of six species, six varieties, and two forms are recognized.

*Schkubria* is entirely American in its distribution with the exception of the few specimens reported from Africa which were probably introduced there. The genus extends in North America from the southwestern United States through Mexico and Guatemala, and in South America from Venezuela and Colombia to Argentina and Chile. Moreover, one species, *S. multiflora*, exhibits a discontinuous distribution between the two continents. It may well be that when more specimens are available for study many of the varieties and forms described herein would better be termed subspecies.

*Schkubria pinnata* and its varieties, and perhaps *S. anthemoidea* to a lesser extent, have some use in popular medicine<sup>11</sup>. According to the labels on many of the specimens the plants are used as insect repellents or insecticides, particularly to kill fleas. *Schkubria* deserves further investigation along these lines. An interesting observation made during this study was that the herbarium specimens of *Schkubria* were quite free of insect damage.

The writer wishes to express his thanks to Dr. George T. Moore, Director, for the use of the facilities of the Missouri Botanical Garden; to Dr. Jesse More Greenman, for his helpful criticism and advice; to Miss Nell C. Horner and other members of the staff of the Missouri Botanical Garden, for their cooperation; to Sr. Angel L. Cabrera of the Museo de La Plata, Argentina; and to Mr. Norlan C.

<sup>8</sup> Rydb., *loc. cit.*, and p. 34.

<sup>9</sup> Gray in *Smithson. Contr. Knowl.* [Pl. Wright.] 5:95. 1853.

<sup>10</sup> Cabrera, *loc. cit.*

<sup>11</sup> O'Donnell and Rodríguez consider *S. pinnata* medicinally in "Las plantas medicinales del noroeste Argentina. II." *Rev. Farm. (Buenos Aires)* 84:149-159. 1942. I have not seen this reference.

Henderson, formerly graduate student, Henry Shaw School of Botany of Washington University. All opinions expressed, however, and any errors are those of the writer. Acknowledgments are made to the herbaria which have loaned specimens for examination. The abbreviations used in this paper are as follows: personal herbarium of A. L. Cabrera (C); Chicago Natural History Museum (formerly Field Museum of Natural History) (FM); Gray Herbarium of Harvard University (G); Missouri Botanical Garden (MBG); Philadelphia Academy of Natural Sciences (PA); University of Texas (T); United States National Herbarium (US).

## TAXONOMY

*Schkuhria* Roth, Cat. Bot. 1:116. 1797; Benth. & Hook. Gen. Pl. 2:403. 1873; Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>b</sup>:260. 1890; Cabrera, Comp. Bonaerenses, in Rev. Mus. La Plata, Secc. Bot. N. S. 4:244. 1941, not *Schkuhria* Moench, Meth. 566. 1794.

*Tetracarpum* Moench, Meth. Suppl. 240. 1802; Rydb. in N. Am. Fl. 34:44. 1914.

*Mieria* Llave in Llave & Lex. Nov. Veg. Desc. 2:12. 1825.

*Achyropappus* Link & Otto, Ic. Pl. Rar. pl. 30. 1829, not *Achyropappus* HBK.

*Hopkirkia* DC. Prodr. 5:660. 1836, not *Hopkirkia* Spreng.

*Cephalobembix* Rydb. in N. Am. Fl. 34:46. 1914.

Slender, branching, erect or decumbent annuals, rarely perennials. Stems glabrate to hispid. Lowermost leaves opposite, upper alternate, pinnately or bipinnately divided into linear-filiform lobes, rarely simple, often impressed-punctate. Heads discoid or radiate with one to few rays. Involucre obconic to turbinate. Bracts of the involucre 4–18, obovate to oblanceolate, rather narrow, scarious and frequently colored on the margins, occasionally one or more smaller bracts present. Ray-flowers 1–3, rarely more, yellow to white, minute. Disk-flowers few to numerous, yellow, rarely red-tipped, lobes 5, extending about half the length of the throat, glandular tube equal to or less than the length of the throat. Style branches with short acute appendages. Achenes elongate, obpyramidal, generally 4-angled, villous or hispid on the angles, particularly at the base. Pappus of 8, rarely more, scarious squamellae, calloused at the base or with prominent mid-rib becoming an awn in some of the species.

Type species: *Schkuhria abrotanoides* Roth = *Schkuhria pinnata* var. *abrotanoides* (Roth) Cabrera.

## KEY TO THE SPECIES, VARIETIES, AND FORMS OF SCHKUHRIA

- A. Ligules lacking; achenes 10 or more.
- B. Plants decumbent, annual; leaves inconspicuously punctate; involucre bracts persistently pubescent.
- C. At least half of the pappus scales (squamellae) awned.
  - D. Awns of the pappus scales 1 mm. or longer; scales colorless..... 3. *S. multiflora*
  - DD. Awns less than 1 mm. long; scales maroon to purplish..... 4. *S. degenerica*
- CC. Pappus scales not awned (except rarely 1 or 2).
- D. Involucral bracts 5–6, 2 (rarely 3) mm. broad; achenes generally less than 15; squamellae rarely longer than 0.5 mm..... 3a. *S. multiflora* var. *pusilla*

- DD. Involucral bracts 7 or more, mostly 1-2 mm. broad; achenes generally more than 15; squamellae frequently longer than 0.5 mm. 3. *S. multiflora*
- BB. Plants erect, perennial; leaves conspicuously punctate; involucral bracts glabrate. 6. *S. Greenmanii*
- AA. Ligule or ligules usually present; achenes 9 or less (except in *S. schkuhrioides*).
- B. Ligules 1 (rarely 2 or lacking), 1-3 mm. long; involucral bracts obovate to lanceolate; squamellae over 0.5 mm. long (except in *S. pinnata* var. *virgata* f. *Pringlei*).
- C. None of the pappus scales awned.
- D. Scales about 2 mm. or longer, equal to subequal.
- E. Achenes short-villous (hairs less than 0.4 mm. long) or hispid on the angles; ligule about 2 mm. long; pappus scales erose; South American plants. 1. *S. pinnata*
- EE. Achenes long-villous (hairs more than 0.4 mm. long) on the angles; ligule about 1 mm. long; pappus scales merely denticulate; plants not of South America. 2d. *S. anthemoidea* var. *Wrightii*
- DD. Scales about 1 mm. long, unequal, those on the angles longer. 1d. *S. pinnata* var. *virgata* f. *Pringlei*
- CC. Half or more of the pappus scales awned.
- D. Disk-flowers 5 or less (rarely 6); achenes long-villous on the angles.
- E. Scales equal to subequal, generally more than half of them awned.
- F. Ligule about 1 mm. long. 2. *S. anthemoidea*
- FF. Ligule about 2 mm. long. 2a. *S. anthemoidea* var. *guatemalensis*
- EE. Scales unequal, only those on the angles awned (rarely 1 or 2 of the intermediate scales awned).
- F. Ligule about 1 mm. long. 2b. *S. anthemoidea* var. *Wisizenii*
- FF. Ligule 2-3 mm. long. 2c. *S. anthemoidea* var. *Wisizenii* f. *flava*
- DD. Disk-flowers 5-8; achenes short-villous on the angles.
- E. All, or all but 1, of the scales awned; plants of South America. 1a. *S. pinnata* var. *octoaristata*
- EE. About half of the scales awned.
- F. Ligule 2 mm. long; pappus scales slightly overlapping; plants of South America. 1b. *S. pinnata* var. *abrotanoides*
- FF. Ligule 1 mm. long; pappus scales not overlapping; plants of Mexico and Central America. 1c. *S. pinnata* var. *virgata*
- BB. Ligules usually more than 2, 3-5 mm. long; involucral bracts broadly obovate; squamellae about 0.5 mm. long. 5. *S. schkuhrioides*

1. *Schkuhria pinnata* (Lam.) O. Kuntze, Rev. Gen. Pl. 3:170. 1898, as synonym of *Rothia pinnata*; Cabrera in Anal. Soc. Cient. Argent. 114:187. 1932.

*Pectis pinnata* Lamarck in Jour. Hist. Nat. 2:150. pl. 31. 1792.

*S. bonariensis* Hook. & Arn. in Hook. Jour. Bot. 3:321. 1841, in part.

*S. isopappus* Benth. Plant. Hartweg. p. 205. 1845.

*Amblyopappus mendocinus* Philippi in Anal. Univ. Chile 36:184. 1870.

*S. coquimbana* Philippi in Anal. Univ. Chile 90:29. 1895.

*Rothia pinnata* a *pallida* O. Kuntze, loc. cit., p. 170, in part.

*R. pinnata* β *purpurascens* O. Kuntze, loc. cit., in part.

*S. abrotanoides* var. *pomasquiensis* Hieron. in Engl. Bot. Jahrb. 29:53. 1900, in part.

*S. advena* Thellung in Fedde, Rep. Sp. Nov. 11:308. 1912.



Erect annual; stems glabrate, striate, 20–50 cm. in height; leaves glabrate, pinnately or bipinnately dissected, or the upper and lower entire, linear, 10–40 mm. long, with the filiform segments 0.5–2 mm. wide, glandular-punctate; heads radiate, numerous, on peduncles 1–5 cm. long; involucre 4–5 mm. high, less wide; involucre bracts 4–5, obovate to oblanceolate, obtuse, punctate, with membranous margins, frequently colored purple, red, or yellow; disk-flowers 5–8, yellow, with tubular corollas; ligules 1, frequently glandular, pistillate, about 2 mm. long; achenes narrow, 3–4 mm. long, about three times as long as broad, hispid to short-villous on the angles, the hairs seldom longer than 0.3 mm.; pappus of 8 muticous scales, mostly unequal, irregular, erose.

Distribution: from Ecuador to Chile and Argentina, 3,000 to 10,000 ft.; elsewhere probably introduced.

ECUADOR—AZUAY: vicinity of Cuenca (from market), *Rose, Pachano & Rose 22829*, in part (G, US). IMBABURA: hills near Ibarra, *Jameson 675* (G, US). PICHINCHA: Andes, Cordillera de Quito, *Jameson 2* (US); "Guapulo prope Quito" (according to Benthams, *loc. cit.*), *Hartweg 1141* (fragment FM, G; photograph FM, G). TUNGURAHUA: vicinity of Ambato, *Pachano 59* (G), *s. n.* (NY, US). PROVINCE NOT DETERMINED: near Pomasqui, *Mille 474* in part (US).

BOLIVIA—COCHABAMBA: Pocona, *Steinbach 8655* (FM, G, MBG); Cereado (?), *Steinbach 9707* in part (FM, MBG); Cochabamba, *Cardenas 740* (US). LA PAZ: vicinity of Sorata, *Bang 1298* (G, MBG, NY, US). TARIJA: Bermejo and Tecumilla, *Fiebrig 2126* in part (G).

PERU—HUANUCO: Huanuco, coll. of 1778–88, *Ruiz & Pavon* in part (NY, US). JUNIN: Mito, *MacBride 3264* (G, US). DEPARTMENT NOT DETERMINED: Uspachaca, *MacBride & Featherstone 1294* (FM, G, US); valley of the Mantaro, *Weberbauer 6469* (US).

BRAZIL—SAO PAULO: Campinas, *Santoro 741* in part (US).

ARGENTINA—BUENOS AIRES: Pergamino, *Parodi 1385* (G). CATAMARCA: Andalgalá, *Jørgensen 1783* (G, MBG, US), *Cabrera 1015* (C). CORDOBA: Córdoba, Aug. 1878, *Hieronymus* (G), *Lossen 56* (G). LA RIOJA: Quachin, *Venturi 7844* (FM, G, MBG, US). JUJUY: Volcán, *Venturi 10192* (MBG), Río Chico, *3412* (G). MENDOZA: Potrerillos, *Ragonese 250* (C). SANTA FE: Arroyo Seco, *Ragonese 252* (C). SAN JUAN: Quebrada de Zonada, *Rodrigo 2925* (C). SAN LUIS: between Merlo and Rincón, Santa Rosa, Feb. 1929, *Cabrera* (FM, US).

CHILE—COQUIMBO: Rivadavia: Río Turbio, *Cabrera 3502* (C). PROVINCE AND LOCALITY NOT DETERMINED: *Philippi 15425* (photograph, FM).

UNITED STATES. MASS.—NORFOLK CO.: Milton, 25 Sept. 1929, *Kidder*<sup>12</sup> (G, US).

MOZAMBIQUE—Lourenco Marques, *Morensen*<sup>13</sup> 18 (US).

1a. *Schkuhria pinnata* var. *octoaristata* (DC.) Cabrera in Anal. Soc. Cient. Argent. 114:190. 1932.

*S. octoaristata* DC. Prodr. 5:654. 1836.

*S. pinnata* β *purpurascens* O. Kuntze, Rev. Gen. Pl. 3:170. 1898, in part.

*S. abrotanoides* var. *isopappa* Hieron. in Engl. Bot. Jahrb. 29:53. 1900, in part.

Ligule 1–2 mm. long; squamellae of the achenes linear-lanceolate, equal, all or all but one of the scales gradually attenuated into an awn, exceeding the disk-corolla in length; otherwise as in the species.

<sup>12</sup> This plant was found growing in Kidder's garden as a weed. See *Rhodora* 31:243. 1929. This specimen was determined as *S. Wrightii* but seems to be more closely related to *S. pinnata*.

<sup>13</sup> This plant seems to be introduced also. It is quite probable that *S. pinnata* var. *abrotanoides* occurs with the typical form here.

Distribution: Ecuador to northern Argentina, 2,000 to 10,000 ft.

ECUADOR—AZUAY: vicinity of Cuenca (from market), *Rose, Pachano & Rose* 22829 in part (G, US). CHIMBORAZO: Riobamba, *Schimpff* 922 in part (G). PROVINCE NOT DETERMINED: Andes, *Spruce* 1789 (FM, G).

BOLIVIA—COCHABAMBA: Cordillera de Tunari, *Eyerdam* 24661 (FM, MBG); Cereado (?), *Steinbach* 9707 in part (G). LA PAZ: La Paz, *Aspland* 4925 (US); vicinity of Sorata, *Mandon* 71 (NY). SANTA CRUZ: Buenavista, *Steinbach* 6937 (FM, G, MBG, NY, PA).

PERU—APURIMAC: Andahuailas, *Herrera* 1492 (G). CUZCO: Cuzco, Feb. 1929, *Herrera* (FM). LIMA: Matucana, *MacBride & Featherstone* 275 (FM, G, US).

ARGENTINA—JUJUY: Jujuy, Oct. 1892, *Kuntze* (US). SALTA: Salta, *Holmberg* 10635 (MBG). SANTIAGO DEL ESTERO: Estancia el Remate, *Venturi* 5836 (US). TUCUMAN: Dept. Burruyaca, *Venturi* 2595 (US); Dept. Crianças, Capia, *Venturi* 1082 (FM, MBG).

1b. *Schkuhria pinnata* var. *abrotanoides* (Roth) Cabrera in Anal. Soc. Cient. Argent. 114:189. 1932.

*S. abrotanoides* Roth, Cat. Bot. 1:116. 1797; DC. Prodr. 5:654. 1836.

*S. bonariensis* Hook. & Arn. in Hook. Jour. Bot. 3:321. 1841, in part.

*Rotbia pinnata* a *pallida* O. Kuntze, Rev. Gen. Pl. 3:170. 1898, in part.

*S. abrotanoides* var. *pomasquiensis* Hieron. in Engl. Bot. Jahrb. 29:53. 1900, in part.

*S. abrotanoides* var. *isopappa* Hieron. loc. cit., in part.

Ligule about 2 mm. long; the squamellae on the angles awned, ovate-lanceolate, almost equalling the length of the disk-corolla; the intermediate scales shorter, unequal to subequal, muticous, slightly overlapping the scales on the angles, all of the squamellae strongly calloused at the base; otherwise as in the species.

Distribution: Venezuela and Colombia to Uruguay and Argentina, 750 to 12,000 ft.

VENEZUELA—PROVINCE NOT DETERMINED: San Rafael de Muchchies, *Pittier* 13346 (NY, PA, US).

COLOMBIA—CUNDINAMARCA: Soacha near Bogotá, *Bros. Apollinaire & Arthur* 109 (G, US). DEPARTMENT NOT DETERMINED: coll. of 1918, *Bro. Joseph* (US, NY), and 9 Aug. 1919, *Guatanita* (US).

ECUADOR—CHIMBORAZO: Riobamba, *Mille* 474 in part (G); western Riobamba, *Schimpff* 922 in part (MBG). PROVINCE NOT DETERMINED: Coquimba and Guayaquil, *Nee*, s. n. (FM).

BOLIVIA—CHUQUISACA: near Sucre, June 1943, *Hein*<sup>14</sup> (US). COCHABAMBA: vicinity Cochabamba, *Bang* 755 (G, MBG, NY, US), *Buchtien* 4803 (US). LA PAZ: Chimasí near Chulumani, *Buchtien* 2442 (US), *Millahuaya*, 4802 (US). TARIJA: Bermejo and Tucumilla, *Fiebrig* 2126 in part (G, US). DEPARTMENT NOT DETERMINED: Contana, *Buchtien* 177 (FM, G, MBG, US); no locality given, *Bridges* s. n. (G).

PERU—AYACUCHO: Hunata, *Killip & Smith* 23335 (NY, US); Prov. Cangallo, Hacienda Pajonal, *Stork & Horton* 10793 (FM). CUZCO: Prov. Calca, Hacienda Urco, *Vargas* 696 (FM). HUANUCO: Huanuco, coll. of 1778-79 in part, *Ruiz & Pavon* (FM, NY). LOCALITY NOT DETERMINED: *Klatt* 654 (G), *Weberbauer* 6449 (FM).

BRAZIL—SAO PAULO: Campinas, *Santoro* 741 in part (US).

URUGUAY—No locality given, March 1876, *Loreato* (NY).

ARGENTINA—BUENOS AIRES: Pergamino, *Parodi* 9581 (G, MBG). LA PLATA: Estacion Cargas, *Cabrera* 7467 (C). CHACO: Villa Angela, *Boffa* 1024 (C). CORDOBA: Río

<sup>14</sup> Note from Hein's herbarium label: "Piquipichana or flea-broom. The uses of this plant are to destroy fleas and to fight all sorts of disease, including malaria. It is taken as an infusion, stems and seed being poured in hot water; this same liquid serves to wet the floor of rooms that are to be disinfected."

Tercero, *Burkhardt 10941* (G, MBG); south of Córdoba, coll. of 1878, *Hieronymus* (G); Córdoba, July 1891, *Kuntze* (NY, US), *Lossen 56* (FM, PA). SALTA: Dept. Rosario and Lerma, Campo Zuipano, *Venturi 8044* (US); Dept. Candelaria, Cerro de Chroville(?), *Venturi 3762* (G, US). SANTA FE: entre Rosacio y Casilda, *Ragonese 302* (C). SAN LUIS: Alto Pencoso, Feb. 1914, *Bruch & Carette* (C, G, US). MENDOZA: Santa Rosa, coll. of 1904-5, *Jensen* (US). TUCUMAN: Leales, *Venturi 7141* (714?) (US).

FRANCE—cultivated in Paris, coll. of 1815, *Gay* (G).

The synonymy of the foregoing species and its two South American varieties is exceedingly involved. The writer has examined type material or photographs of types of many of these entities and finds it best to cite them at this time "in part" under more than one heading.

1c. *Schkuhria pinnata* var. *virgata* (Llave) Heiser, n. comb.

*Mieria virgata* Llave in Llave & Lex. Nov. Veg. Descr. 2:12. 1825.

*S. virgata* DC. Prodr. 5:654. 1836.

*Tetracarpum virgatum* Rydb. in N. Am. Fl. 34:45. 1914.

*Schkuhria glabrescens* Gandoger in Bull. Soc. Bot. Fr. 65:46. 1918.

Ligule about 1 mm. long; the squamellae of the pappus awned on the angles, lanceolate, shorter than the disk-corolla, the intermediate scales generally less than half as long, muticous, equal to subequal, not overlapping the other scales, only weakly calloused at the base; otherwise as in the species.

Distribution: northern Mexico to Guatemala, 5,000 to 9,000 ft.

MEXICO—AGUASCALIENTES: Rincón de Romos, *Shreve 9247* (G). CHIHUAHUA: Río Mayo, *Gentry 1926* (FM, G, MBG, US); near Guerrero, *Pringle 1292* in part (PA), Sierra Madre, Arroyo Ancho, *7082* (G, US). DURANGO: City of Durango and vicinity, *Palmer 509* (G, MBG, NY, US). FEDERAL DISTRICT: near Mexico, *Berlandier s. n.* (G, MBG); Mexico City, *Orcutt 4072* (FM, G, MBG); Lomas de Santa Fé, *Lyonnet 408* (MBG, NY, US); Tlalpam, *MacDaniels 46* (FM); Cerro de Guadalupe, *Pringle 8724* (G, MBG, NY, PA, US), vicinity of Mexico, *7928* (G, MBG, US). GUANAJUATO: Obregon, *Seler 1133* (G, NY, US). HIDALGO: hills above Pachuca, *Pringle 6943* (G, MBG, NY, PA, US); between Pachuca and Real del Monte, *Rose & Painter 6715* (NY, US); Real del Monte, *Ehrenberg 375a* (G). MEXICO: Valle de Mexico, *Bourgeau 372* (G, US); hills above Toluca, *Pringle 9096* (MBG, US); Temascaltepec, Mina de Agua, *Hinton 1405* (MBG, US), Pantoja, *6228* (G, NY). MICHOACAN: vicinity of Morelia, *Kenoyer A127* (FM). PUEBLA: vicinity of Puebla, *Arsène 352* (US), *2315* (MBG, NY, US), s. of Puebla, n. of Hacienda Batán, *1462* (US), Laguna de San Baetasar, 1 Aug. 1909 (US), and Cerro San Juan, 15 Aug. 1906 (US); Cerro del Corral de Piedra, near Oaxaca, *Purpus 3836* (FM, MBG, NY, US). SAN LUIS POTOSI: region of San Luis Potosi, *Parry & Palmer 427* in part (MBG, NY, PA, US); San Luis Potosi, *Schaffner 332* (750) (NY, US). ZACATECAS: near Plateado (Plateros?), *Rose 2748* (US). LOCALITY NOT DETERMINED: *Coulter 314* (G, NY, PA), *Muller 1163* (NY), *Berlandier 708* (fragment FM), *Bonpland s. n.* (FM).

GUATEMALA—HUEHUETENANGO: Chacula, *Seler 2870* (G, US).

*Schkuhria virgata* DC. is best interpreted as a Central American variety of *S. pinnata*, for the only reliable difference lies in the nature of the pappus.

1d. *Schkuhria pinnata* var. *virgata* f. *Pringlei* (S. Wats.) Heiser, n. comb.

*S. Pringlei* S. Wats. in Proc. Am. Acad. 23:278. 1888.

*Tetracarpum Pringlei* Rydb. in N. Am. Fl. 34:44. 1914.

As the variety but the squamellae very short, less than 1 mm. long, those on the angles frequently somewhat awned, the intermediate scales still smaller, muticous.

Distribution: Chihuahua and Durango, Mexico.

MEXICO—DURANGO: along road from Durango to Santa Cruz, *Langman* 2956 (PA). CHIHUAHUA: Majalca, *Le Sueur* 1228 (FM), Cima (FM, T); southwestern Chihuahua, *Palmer* 387 (NY, PA, US); base of Sierra Madre, *Pringle* 1639 (MBG, NY), near Guerrero, 1292 in part (G, US).

It is worthy of note that in South America certain specimens of *S. pinnata* and its variety *abrotanoides* occur which have a pappus almost identical with that of the above form. I have not separated these specimens (*Venturi* 8044 in part, *Steinbach* 8655 in part) from the variety, but it is interesting to observe their parallel development. *S. anthemoidea* var. *Wrightii* in Texas also occurs with a very reduced pappus which resembles this form somewhat. I choose to regard *S. Pringlei* S. Wats. simply as a form of *S. pinnata* var. *virgata*, for the only constant difference is found in the size of the squamellae.

2. *Schkuhria anthemoidea* (DC.) Coul. in Donn-Smith, Enum. Pl. Guat. 4:93. 1895, in part, as "*anthemoides*" sphalm.

*Hopkirkia anthemoidea* DC. Prodr. 5:660. 1836.

*S. Hopkirkia* Gray in Smithson. Contr. Knowl. [Pl. Wright] 5:94. 1853.

*Tetracarpum anthemoideum* Rydb. in N. Am. Fl. 34:45. 1914.

Erect annual; stems glabrate, striate, 20–50 cm. in height; leaves glabrate, pinnately or bipinnately dissected into linear filiform segments, 10–40 mm. long, 0.5–2 mm. wide, or the upper and lower entire, conspicuously glandular-punctate; heads radiate, numerous, on peduncles 1–5 cm. long; involucre 5–7 mm. high, less wide; involucre bracts 4–5, obovate, obtuse, glabrous, punctate, green with scarious colored margins, deep purple to red; disk-corollas rarely more than 5, yellow, rarely red-lobed; ligule 1, pistillate, about 1 mm. long; achenes 3–4 mm. long, about twice as long as broad, thick, striate, densely villous on the 4 angles, the hairs 0.4 mm. or longer; squamellae equal to subequal, ovate-lanceolate to lanceolate, most or all of the scales awn-tipped, about the length of the disk-corolla or only slightly exceeding it.

Distribution: Arizona to southern Mexico, 2,000 to 8,000 ft.

UNITED STATES—ARIZONA: COCHISE CO.: Chiricahua Mts., top of main ridge between Rock and Turkey creeks, *Blumer* 1635 in part (G, NY); n. of Fort Huachuca, *Lemmon* 4774 (G); Huachuca Mts., *Lemmon* 2779 (US); Sunnyside, *Kearney & Peebles* 13834 (US).

MEXICO—CHIAPAS: between Tuxtla and San Cristobal, *Nelson* 3122 (US). CHIHUAHUA: Rio Mayo, Cerro Quicorichi, *Gentry* 1924 (FM, G, MBG, US); near Chihuahua, *Pringle* 772 (G, MBG, NY, PA, US), hills around Parral, 13566 (G, US). COLIMA: Alzada, *Orcutt* 4625 (FM, MBG). FEDERAL DISTRICT: Olivar, *Orcutt* 3683 (FM); pyramid of Cuicuilco, Tlalpam, *McDaniels* 719 (FM); Tlalpam, *Seler* 4111 (G, US); hills north of Mexico City, *Pringle* 6781 (G, MBG, NY, PA, US), Cerro de Guadalupe, 9957 (NY). GUANAJUATO: valley of Silao, 24 kilo. s. of Guanajuato, Nov.-Dec. 1893, *Duges* (G). GUERRERO: Tasco, *Abbott* 447 (G). JALISCO: Lake Chapala, *Lemmon* 76 (G); Tequila, *Palmer* 365 (G, MBG, NY, PA, US); hills above Etzatlán, *Pringle*

11568 (G, US). MEXICO: Molino, *McDaniels* 587 (FM), *Rose & Painter* 6979 (FM, MBG, NY, US); near Cuernavaca, *McDaniels* 333 (FM), *Rose & Hough* 4445 (US). NAYARIT: Cerro de la Cruz, e. of Tepic, *Ynes Mexia* 657 (G, FM, MBG, NY, US). OAXACA: coll. of 1922, *Reko*<sup>15</sup> (US). PUEBLA: vicinity of Puebla, Cerro Guadalupe, *Arsène* 1869 (MBG, US), Fort Guadalupe, 86 (US), Cerro and Fort Guadalupe, 1198 (US). SONORA: Cañon de Aribabi, south of Aribabi, *White* 2747A (G). VERA CRUZ: Orizaba, *Miller* 270 (US); Corral de Piedras, *Purpus* 8241 (G, MBG, NY, US). STATE NOT DETERMINED: *Haenke* (photograph of TYPE, FM).

2a. *Schkuhria anthemoidea* var. *guatemalensis* (Rydb.) Heiser, n. comb.

*S. virgata* Hemsl. Biol. Centr.-Am. Bot. 2:212. 1881, in part.

*S. anthemoidea* Coult. in Donn.-Smith, Enum. Pl. Guat. 4:93. 1895, in part.

*Tetracarpum guatemalense* Rydb. in N. Am. Fl. 34:45. 1914.

*S. guatemalensis* Standl. & Steyermark in Field Mus. Publ. Bot. 22:319. 1940.

Involucral bracts generally reddish or purplish at the apex; ligule about 2 mm. long; disk-flowers 4-6; squamellae subequal, mostly ovate-lanceolate, 4-7 of the scales awned, equalling or slightly shorter than the disk-corolla, always strongly calloused at the base; otherwise as in the species.

Distribution: Guatemala and El Salvador, 1,500 to 8,000 ft.

GUATEMALA—AMATITLAN: Canchalagua, Laguna, *Ruano* 1294 (FM); Canchalagua, Morales 792 (US). CHIQUIMULA: llanos around Ipala, *Steyermark* 30316 (FM, NY). GUATEMALA: Estancia Grande, *Standley* 59186 (FM, NY); Finca Bretana, road between Guatemala and Fiscal, *Standley* 59757 (FM). HUEHUETENAGO: Aguacatan road, 10 km. e. of Huehuetenango, *Standley* 82115 (FM); no locality given, *Skutch* 1589 (G). JALAPA: Laguna de Ayarza, *Heyde & Lux* 3802 (FM, G, MBG, NY, US); between Jalapa and base of Volcán Jumay, *Steyermark* 32259 (FM). JUTIAPA: n. of Jutiapa, *Standley* 60512 (FM). DEPARTMENT NOT DETERMINED: "La Aurora," *Ruano* 568 (US); no locality given, *Tonduz* 885 (G, NY, US).

EL SALVADOR—AHUACHAPAN: *Padilla* 235 (MBG, NY, US). SANTA ANA: near Chalchuapa, *Calderón* 962 (FM, MBG, NY, US). DEPARTMENT NOT DETERMINED: *Renson* 305 (FM, G, NY, US); La Cebadilla, *Calderón* 1236 (G, US).

I can regard this plant only as a variety of *S. anthemoidea*, from which it can be distinguished only with difficulty if the locality of the collection were unknown.

2b. *Schkuhria anthemoidea* var. *Wislizenii* (Gray) Heiser, n. comb.

*S. Wislizeni* Gray in Mem. Am. Acad. II. 4:96. 1849.

*Tetracarpum Wislizeni* Rydb. in N. Am. Fl. 34:45. 1914.

Involucral bracts yellow to purple at the apex; ligule seldom over 1 mm. long, almost as wide; squamellae lanceolate to ovate-lanceolate, those on the angles awn-tipped, the intermediate ones shorter, muticous.

Distribution: Arizona to central Mexico, 5,000 to 8,000 ft.

UNITED STATES. ARIZONA—COCHISE CO.: Chiricahua Mts., top of main ridge between Rock and Turkey creeks, *Blumer* 1634 (FM, G, MBG, NY, US); Mule Mts., *Harrison & Kearney* 6224 (G, US).

MEXICO—CHIHUAHUA: Mojarachic, *Knobloch* 5464 (FM), southwestern Chihuahua, *Palmer* 387 (G); hills about Parral, *Pringle* 13567 (G, US); Cosihuinachic Mts., *Wis-*

<sup>15</sup> Note from herbarium label: "Brooms of plants sold in markets, used for exterminating fleas."



*lizenus* 195 (TYPE COLLECTION G, MBG). FEDERAL DISTRICT: Cerro de Guadalupe, *Pringle* 9957 (G, MBG, US). HIDALGO: Pachuca, *Orcutt* 3921 (FM, G, MBG).

2c. *Schkuhria anthemoidea* var. *Wislizenii* f. *flava* (Rydb.) Heiser, n. comb.

*Tetracarpum flavum* Rydb. in N. Am. Fl. 34:46. 1914.

As the variety but the ligule 2–3 mm. long, less broad.

Distribution: southern Mexico. (I have examined this form only from Oaxaca at altitudes from 5,000 to 7,500 ft.)

MEXICO—OAXACA: District of Etlá, Las Sedas, *Conzatti* 5004 (MBG); Oaxaca, *Galeotti* 2049 (2045?) (G); Reyes, *Nelson* 1710 (US); limestone hills near Etlá, *Pringle* 4881 (G, MBG, NY, PA, US); Sierra de San Felipe, *Smith* 263 & 626 (TYPE COLLECTION MBG, US).

This species of Rydberg's is no more than a form differing from the variety only in the length of the ligule.

2d. *Schkuhria anthemoidea* var. *Wrightii* (Gray) Heiser, n. comb.

*S. Wrightii* Gray in Smithson. Contr. Knowl. [Pl. Wright.] 5:95. 1853.

*Tetracarpum Wrightii* Rydb. in N. Am. Fl. 34:44. 1914.

Ligule about 1 mm. long; disk-flowers 5 or less; squamellae obovate, subequal, rounded at the apex, denticulate; otherwise as in the species.

Distribution: southwestern United States and northwestern Mexico, 3,500 to 7,500 ft.

UNITED STATES. ARIZONA—COCHISE CO.: Chiricahua Mts., top of main ridge between Rock and Turkey creeks, *Blumer* 1635 in part (MBG, NY, US); Silver Creek, Chiricahua National Park, *Eggleston* 10935 (G, US); Mule Mts., *Harrison & Kearney* 6088 (G); Ramsey Canyon, Huachuca Mts., *Jones* 25041 (G), and 29 Sept. 1929 (MBG); Apache Pass, Chiricahua Mts., Sept. 1881, *Lemmon* (MBG); plain near Ft. Huachuca, *Peebles, Harrison & Kearney* 3468 in part (US); base of the Huachuca Mts., 15 Sept. 1884, *Pringle* (G, NY, PA, US); near Fort Huachuca, *Wilcox* 334 (NY, US). PIMA CO.: Greaterville, *Sbreve* 4973 (MBG). SANTA CRUZ CO.: Sonoita, *Harrison & Kearney* 5703 (US). NEW MEXICO—DONA ANA CO.: Organ Mts., 4 Sept. 1898, *Cockerell* (US), *Wootton* 445 (G, MBG, NY, US), 28 Sept. 1902 (MBG), and 20 Sept. 1908, *Wootton & Standley* (US). GRANT CO.: (?) near Santa Rita de Cobre, 21 Sept. 1880, *Greene* (MBG, NY). SIERRA CO.: Fruijilla Creek, *Metcalf* 1358 (G, MBG, NY, US); Lake Valley, coll. of 1916, *Beals* (US). TEXAS—JEFF DAVIS CO.: Davis Mts. near Mt. Locke, *Hinckley* 478 (FM, NY), Mt. Livermore, 28 Sept. 1935 (FM, T); Davis Mts., *Palmer* 30652a (MBG, PA, T), 19 Sept. 1918, *Young* (T); Limpia Cañon, *Nealley* 189 (FM); 5 mi. n. w. of McDonald Observatory, *Innes & Moon* 1133 (G); Ft. Davis, 23 Aug. 1941, *Strandtmann* (T).

MEXICO—CHIHUAHUA: San Diego Cañon, Sierra Madre Mts., 16 Sept. 1903, *Jones* (NY); 30 mi. s. w. of Chihuahua, *Muller* 3341 (G); vicinity of Chihuahua, *Palmer* 346 (US); rocky hills near Chihuahua, *Pringle* 607 (G, MBG, NY, PA, US), 772 in part (PA), hills near Chihuahua, 974 (MBG, NY), mesas near Carretas, 2001 (G, US), dry hills, Parral, 10113 (G, MBG, NY, PA, US); eastern Chihuahua, just east of Orgaños, *Stewart & Johnston* 2015 (G); Santa Eulalia, 30 Sept. 1885, *Wilkinson* (US). SONORA: San Pedro, *Hartman* 854 (G); no locality given, *Wright* 1254 (TYPE COLLECTION G, PA).

3. *Schkuhria multiflora* Hook. & Arn. in Hook. Jour. Bot. 3:332. 1841.

*Achyroappus schkuhrioides* Don. ex Hook. & Arn., loc. cit., not *Achyroappus*

*schkubrioides* Link & Otto.

- S. Neo-Mexicana* Gray in Mem. Am. Acad. II. 4:96. 1849.  
*Amblyopappus Neo-Mexicanus* Gray in Torr. Pacif. R. R. Rept. 4:106. 1857.  
*Babia Neo-Mexicana* Gray in Proc. Am. Acad. 19:27. 1883.  
*Babia Gilliesii* Gray, loc. cit., p. 28.  
*S. pusilla* var. *aristata* R. E. Fries in Nova Acta Soc. Sci. Upsal. IV. 11:85. t. 6, 8, 1905.  
*Achyropappus neo-mexicanus* Rydb. Fl. Colo. 377. 1906.  
*Cephalobembix neo-mexicana* Rydb. in N. Am. Fl. 34:46. 1914.  
*S. pusilla* var. *longepedicellata* Hauman in Anal. Soc. Cient. Argent. 86:328. 1918.  
*S. multiflora* var. *aristata* Cabrera in Anal. Soc. Cient. Argent. 114:193. 1932, as "multiflora" sphalm.

Annual, more or less decumbent, 5–25 cm. in height; stems short-glandular-hairy to glabrate; leaves pinnately dissected into lobes 0.5–1 mm. wide, up to 3 cm. long; petioles 0.2–1 cm. long; peduncles glandular-pubescent, 0.5–3 cm. long; heads discoid; involucre turbinate to obconic, 5–10 mm. wide, 5–6 mm. high; bracts of the involucre 7–9, green, scarious-tipped, frequently red or yellow on the margins, 1–2 mm. wide and narrowing gradually; disk-corollas 15–30, yellow, occasionally red-tipped; achenes black with a few scattered hairs on the faces, white-villous on the 4 angles, 3–4 mm. long; squamellae 1–2 mm. long, obtuse to acutish, rarely several or all of the squamellae awned, usually strongly calloused at the base.

Distribution: southwestern United States into northern Mexico in North America and Bolivia to Argentina and Chile in South America, 5,000 to 11,000 ft.

UNITED STATES. ARIZONA—NAVAJO CO.: between Kayenta and Betatakin, *Eastwood & Howell* 6574 (FM). YAVAPAI CO.: Prescott, *Griffiths* 7349 (MBG). COLORADO—HUEFANO CO.: Huertano, *Parry* 124, 125 (MBG). RIO GRANDE CO.: banks of the Rio Grande near Del Norte, *Brandege* 1228 (MBG), 12 mi. below Del Norte on the banks of the Rio Grande, 4248 (MBG). NEW MEXICO—LINCOLN CO.: White Mts., *Wootton* 297 (MBG). SAN MIGUEL CO.: near Pecos, *Standley* 5052 (MBG). SANTA FE CO.: Santa Fe, *Fendler* 416 (MBG), *Mulford* 1366 (MBG); southeast of Santa Fe, 9 Sept. 1881, *Engelmann* (MBG); no locality given, *Brandege* 12070 (MBG). SOCORRO CO.: Mogollon Mts., on or near west fork of Gila R., *Metcalf* 580 (MBG). VALENCIA CO.: Cubero, *Rusby* 706 (PA). TEXAS—BREWSTER CO.: Chisos Mts., *Mueller* 8232 (FM, G, MBG, NY, T, US).

MEXICO—CHIHUAHUA: Potrero Mts., *Pringle* 773 (MBG); Majalca, *LeSueur* 1229 (FM, MBG); near Colonia Garcia in the Sierra Madre, *Townsend & Barber* 286 (MBG).

BOLIVIA—LA PAZ: La Paz, *Buchtien* 4802, 9227 (G, MBG).

PERU—AREQUIPA: Arequipa, *Pennell* 13051, 13162 (FM, G, US). MOQUEGUA: Torata, *Weberbauer* 7408 (US).

ARGENTINA—MENDOZA: Potrerillos, *Ragonese* 248 (C). TUCUMAN: Valle de Tafi, coll. of 1908, *Bruch* (C, US).

CHILE—ATACAMA: Dept. Vallenar, Rio de la Laguna Grande, above the mouth of Rio Lag. Chica, *Johnston* 5889 (G, US). PROVINCE NOT DETERMINED: (Chilecito?), *Gillies s. n.* in part (G).

Notwithstanding the discontinuous distribution of *S. multiflora* and *S. neo-mexicana* the two appear to be the same species. This species appears to be very closely related to certain species of *Babia* but lacks the rays typical of that genus. For this type of distribution see I. M. Johnston, Jour. Arn. Arb. 21:336. 1940.

The problem of the relationship between the aristate and the non-aristate specimens of this species can only be more clearly determined when more speci-

mens are available for study. *Buchtien* 4802, 9227 in part, *Weberbauer* 7408 in part, and *Gillies* s. n. in part, have the pappus provided with four or more awns. In a letter to the author Cabrera writes: "The forms with aristas may be possibly included under the name *S. multiflora* var. *typica* as the original diagnosis gives four mutic and four aristate paleae." Owing to the apparently continuous variation it is probably best at present to include the aristate forms with the species. It is worthy of note to point out that so far no North American specimens of *S. multiflora* have been found with aristate squamellae.

3a. *Schkuhria multiflora* var. *pusilla* (Wedd.) Cabrera in Anal. Soc. Cient. Argent. 114:192. 1932.

*S. pusilla* Wedd. Chloris Andina, p. 17, t. 14, B. 1855.

*Rotbia pusilla* O. Kuntze, Rev. Gen. Pl. 3:170. 1898.

*S. pusilla* var. *longepedicellata* Hauman in Anal. Soc. Cient. Argent. 86:328. 1918, in part.

Annual, 1–10 cm. in height; petioles rarely longer than 5 mm.; peduncles 0.2–0.5 cm. long; involucre about 5 mm. high and rarely wider; involucre bracts 5–6, 1–3 mm. wide, olive-green, frequently with yellow (rarely purple) scarious edges; disk-corollas 10–20; achenes about 3 mm. long; squamellae mostly obtuse, 0.5–1 mm. long; otherwise as in the species.

Distribution: Bolivia to Argentina, 8,000 to 12,000 ft. The variety appears to grow at slightly higher altitudes than the species, perhaps accounting in part for its smaller size.

BOLIVIA—LA PAZ: La Paz, *Buchtien* 3069 (US), Cerro de Calvoirio, 707 (US). POTOSI: no locality given, *Cardenas* 433 (US). PROVINCE AND LOCALITY NOT DETERMINED: *Mandon* 73 (FM, NY).

PERU—PUNO: vicinity of Lake Titicaca, *Shepard* 41 (G, NY, US); Chuquibambilla, *Pennell* 13364 (FM, PA).

ARGENTINA—CATAMARCA: Dept. of Andalgalá, El Candado, *Jørgensen* 1282 (G, MBG, US). SALTA: El Alisal, Cerro del Cajón, *Rodriguez* 1422 (C). TUCUMAN: Dept. of Chicligasta, *Venturi* 3298 (US).

COUNTRY AND LOCALITY NOT DETERMINED: *Weddell* 4415 (FM).

I have not seen the type of *Rotbia intermedia* of Kuntze, but it is quite probable that it may fall into synonymy under this variety.

4. *Schkuhria degenerica* (O. Kuntze) R. E. Fries, Arkiv för Bot. 5<sup>12</sup>:22. 1906.

*S. pusilla* var. *major* Schz. Bip. in Bull. Soc. Bot. Fr. 7:80. 1865; Linnaea 34:529. 1866, *nomen nudum*.

*S. oolepis* Schz. Bip. loc. cit., *nomen nudum*.

*Rotbia degenerica* O. Kuntze, Rev. Gen. Pl. 3:169. 1893.

Decumbent annual, 10–40 cm. in height; stem lightly glandular-villous; leaves alternate, pinnately or bipinnately divided into divisions about 1 cm. wide; heads discoid on peduncles 1.0–1.5 cm. long; involucre turbinate, 7–9 mm. long, 1 cm. or less wide; involucre bracts 5–7, green, hispidulous, with a scarious yellow, rarely purplish, apex; achenes 30–40, narrow, weakly 4-angled, more or

less compressed, short-villous on the angles, more densely so at the base, 3–4 mm. long; squamellae 2.0–3.5 mm. long, about 1 mm. wide, slightly exceeding the disk-corolla in length, erose, with a reddish-maroon midrib projected into an awn in about one-half of the squamellae.

Distribution: known only from Bolivia.

BOLIVIA—COCHABAMBA: Cochabamba, *Bang* 966 (FM, G, MBG, PA, US). LA PAZ: Prov. Larecaja, San Pedro near Sorata, *Mandon* 72 (G, FM).

5. *Schkuhria schkuhrioides* (Link & Otto) Thellung in Fedde, Rep. Sp. Nov. 11:308. 1912.

*Achyropappus schkuhrioides* Link & Otto, Ic. Pl. Rar., p. 59, pl. 30. 1829, not

*Achyropappus schkuhrioides* Don. ex. Hook. & Arn.

*S. senecioides* Nees, Del. Sem. Hort. Bot. Bonn. 1831.

*Babia schkuhrioides* Gray in Proc. Am. Acad. 19:27. 1883.

*Tetracarpum schkuhrioides* Rydb. in N. Am. Fl. 34:46. 1914.

Erect annual, 40–80 cm. in height; stem striate, grooved, glabrate; leaves pinnately dissected into narrow linear divisions, 3–7 cm. long, punctate; heads radiate on peduncles 2–5 cm. long; involucre bracts 6–8, obovate to ovate, with yellow scarious tips, frequently subtended by 1 or more smaller bracts; ligules 1–4, obovate-cuneate, 3–5 mm. long; disk-corollas 15–20, yellow with glandular tubes; achenes elongate-obpyramidal, about 3–4 mm. long, with a few short hairs on the angles; squamellae obovate, about 0.5 mm. long.

Distribution: central and southern Mexico.

MEXICO—DURANGO: Durango, *Palmer* 576 (MBG, NY). MEXICO: vicinity of Mexico, *Pringle* 9855 (MBG, NY). MICHOACAN: vicinity of Morelia, *Arsène* 5723 in part (G), Loma Santa Maria, 5837 (FM, G, MBG, NY, US), Lieux (?) in Andes, 3127 (MBG, US); vicinity of Lerma, north of La Piedad, *Pringle* 3281 (MBG, NY).

This species is a connecting link with *Babia*. The glandular-punctate leaves and bracts and the small number of ligules have led me to retain it in *Schkuhria*. The pappus most nearly resembles that of *S. pinnata* var. *virgata* f. *Pringlei*, but on the basis of the appearance and number of achenes *S. schkuhrioides* is more closely related to *S. multiflora*.

6. *Schkuhria Greenmanii* Heiser, n. sp.

Herba perennis, 35–65 cm. alta; caulibus glandulari-punctatis; foliis alternis, pinnato-dissectis, raro simplicibus, segmentis linearibus vel filiformibus, obtusis, impresso-punctatis, 2–7 cm. longis; capitulis homogamis, 1 cm. altis, usque ad 0.5 cm. latis; involucri bracteis 4–5, obovatis apice obtusissimis, marginibus scariosis et fimbriatis; ligulis nullis; disci floribus 10–20, corollis 5-dentatis, 2–4 mm. longis; achaeniis ca. 3 mm. longis, sparse hirsutis vel ad angulos adpresso-pubescentibus; pappi paleis plerumque 8, 3 mm. longis, lanceolatis, dentatis, aristulatis, 1-nerviis, nervo-medio prominente.

Erect perennial, 35–65 cm. in height; stems striate, glabrate, glandular-punctate; leaves mostly alternate, pinnately dissected into linear-filiform divisions, conspicuously glandular-dotted, rarely entire; heads discoid on peduncles 2–5 cm. long; involucre about 1 cm. high, less wide, turbinate, bracts of the involucre 4–5,

more or less keeled at the base, obovate, margins scarious and provided with a fringe; disk-flowers 10-20 with yellow corolla and glandular tube; achenes 4-angled, lightly hirsute on the angles, more so at the base, about 3 mm. long; squamellae usually 8 (7-10), lanceolate, erose on the margins, provided with a conspicuous midrib extending into an awn, 3 mm. long, almost equalling the length of disk-corolla.

MEXICO—MEXICO: District of Temascaltepec, Luvianos, *Hinton 4507* (MBG TYPE; co-types at G, NY, US).

This plant is the only perennial *Schkubria* known, and on the basis of the pappus seems most closely related to *S. anthemoides*, under which name it was originally determined. It also has certain affinities with *Bahia*, from which it is distinct by the lack of ray-flowers.

#### EXCLUDED NAMES AND SPECIES

- Schkubria anthemoides* Wedd. ex Hook. & Jacks. Ind. Kew. 4:827. 1895, as synonym = *Achyropappus anthemoides* HBK. Nov. Gen. & Sp. 4:259. 1820, not *S. anthemoides* of Coult.
- S. Bigelovii* Gray in Proc. Am. Acad. 9:199. 1874. = *Bahia Bigelovii* Gray in Torr. Bot. Mex. Bound. p. 96. 1859. This species is probably best retained in *Bahia* for the present. It is closely related to *S. multiflora*.
- S. biternata* Gray in Proc. Am. Acad. 9:199. 1874. = *Bahia biternata* Gray in Smithson. Contr. Knowl. [Pl. Wright.] 5:95. 1853.
- S. glomerata* Rob. & Seat. in Proc. Am. Acad. 28:109. 1893 = *Florestina pedata* (Cav.) Cass. in Dict. Sci. Nat., Planch. Bot. Dicot. 61:t.86. 1816-29.
- S. integrifolia* Gray in Am. Nat. 8:213. 1874; *Bahia nudicaulis* Gray in Proc. Am. Acad. 19:27. 1883; *Bahia integrifolia* Macbr. in Contr. Gray Herb. 56:39. 1918. = *Platyschkuhria integrifolia* Rydb. in Bull. Torr. Bot. Club 33:155. 1906.
- S. pedata* Gray in Proc. Am. Acad. 9:199. 1874. = *Bahia pedata* Gray in Smithson. Contr. Knowl. [Pl. Wright.] 3:123. 1852.
- S. platyphylla* Rob. & Greenm. in Am. Jour. Sci. 50:156. 1895. = *Florestina platyphylla* Rob. & Greenm. in Proc. Am. Acad. 32:49. 1896.
- Schkubria Schiedei* Gandoger in Bull. Soc. Bot. Fr. 65:46. 1918. I have not seen a specimen of this plant, but from Gandoger's very scanty description it may not even be a *Schkubria*. I can not recognize this species.
- S. viscosissima* Standl. & Steyerl. in Field Mus. Publ. Bot. 22:318. 1940 = *Florestina viscosissima* (Standl. & Steyerl.) Heiser, n. comb. The affinities of this plant are with *F. pedata* (Cav.) Cass., and the nature of the style clearly places it in the genus *Florestina*.
- S. Woodhousei* Gray in Proc. Am. Acad. 19:199. 1874; *Picradeniopsis Woodhousei* Rydb. in Bull. Torr. Bot. Club 37:333. 1910. = *Bahia Woodhousei* Gray in Proc. Am. Acad. 19:28. 1883.



# MULTI-DIMENSIONAL GRAPHICAL REPRESENTATION FOR ANALYZING VARIATION IN QUANTITATIVE CHARACTERS

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AND CHARLOTTE ALPER

A basic difficulty in analyzing data on species crosses is that the mind is ordinarily incapable of comprehending the simultaneous occurrence of variation in several different characters. In studying the results of a cross between *Nicotiana Langsdorfii* and *N. alata*, the authors developed a graphical method for analyzing the variation in four distinct characters considered together.

The four characters used are all measured in the flower, for, as East pointed out in a classic paper on the subject<sup>1</sup>, floral dimensions are better than vegetative

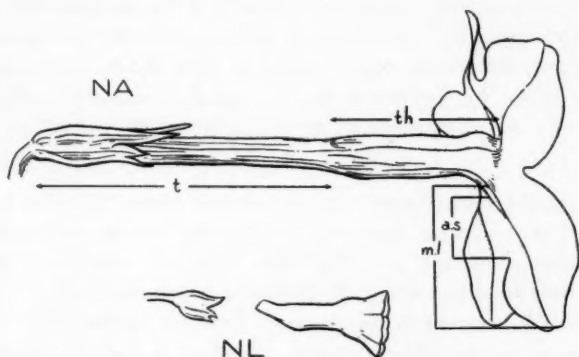


Fig. 1. Flowers of *Nicotiana alata* (NA) and *N. Langsdorfii* (NL):  
t — tube, th — throat, ml — maximum lobe, as — adjacent sinus.

parts for studies of so-called quantitative characters and measurements. These four characters are: the length of throat, maximum lobe, adjacent sinus<sup>2</sup>, and tube (fig. 1), each one being expressed by a different dimension of a fourth-dimensional figure. Thus, the length of the throat is the length of the horizontal, or first dimension; maximum lobe, the vertical or second dimension; adjacent sinus, the third dimension; and tube, the fourth. A fourth-dimensional picture of each generation—the two parents, *Nicotiana Langsdorfii* (NL) and *N. alata* (NA), the F-1 generation (NLA), and two sister families of the F-2 (NLALA-b

<sup>1</sup> East, E. M. Significant accuracy in recording genetic data. *Amer. Jour. Bot.* 3:211-222. 1916.

<sup>2</sup> Smith, Harold H. The relation between genes affecting size and color in certain species of *Nicotiana*. *Genetics* 22:361-375. 1937.

and NLALA-g)—is obtained by using the group's median measurements of each character. To permit accurate comparison, the same scales and angles of slope are used throughout.

As may be seen in fig. 2, extreme dissimilarities in size and shape occur in the parent species, NL and NA, which differ significantly in all six ratios. The greatest difference in proportions is due to the throat being the longest absolute dimension in NL, and the tube longest in NA.

The F-1 and F-2 generations occupy an intermediate position between NL and NA, with the F-1 exhibiting the effects of hybrid vigor by its slightly larger size (very nearly proportionately so) than the F-2. The intermediate condition of the F-1's and F-2's is further emphasized by the approximately equal lengths of tube and throat. The individuals of any F-2 between two very unlike parents will be segregating for various characters which will affect survival differentially, even under experimental conditions. There will be susceptibility to various diseases and environmental conditions—in this case wilt and mosaic, crowding in the seed-pan, survival during cloudy weather in short days of winter, etc. Besides supplying a means for comparing the F-1 and F-2 generations, this graphical method permits the comparison of the F-2's in successive years to obtain an average.

This multi-dimensional representation not only allows the mind to conceive the effects of more than one character at a time, but also permits analysis of just those characters considered, excluding those characters which may, in analyses using the actual flower, cause optical illusions and distracting effects. Additional and more detailed comparisons may be made from the figures—such as variation in actual size of one particular character, the effect of similarity in size of two or three characters, the combined effect of variation in two, three, or four characters. From this treatment of the data it is also obvious that more than four dimensions (or characters) may be considered simultaneously.

The authors wish to thank Dr. Edgar Anderson for many helpful suggestions and the use of his data.

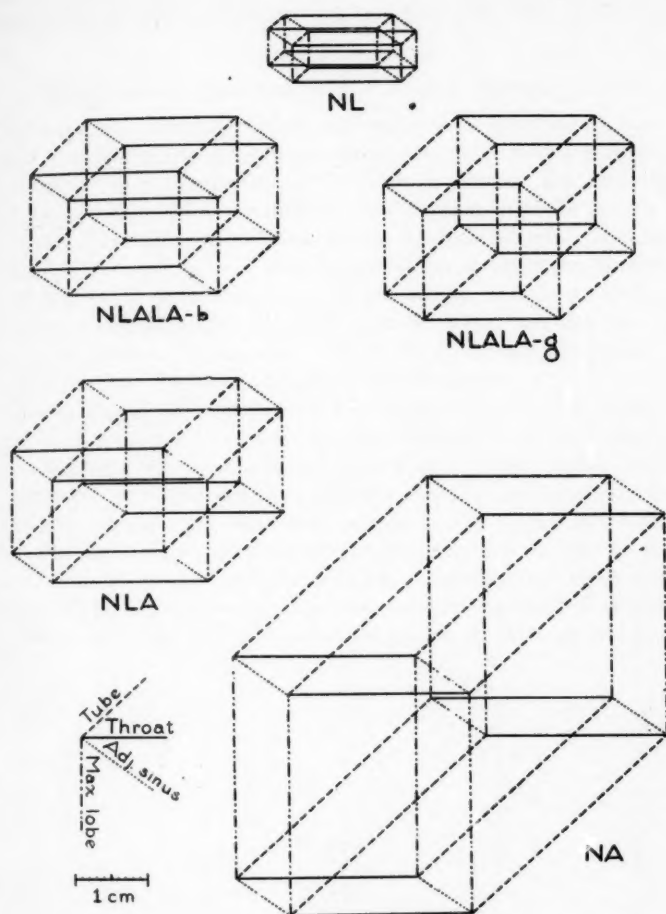


Fig. 2. Fourth-dimensional representation of species crosses in *Nicotiana*.

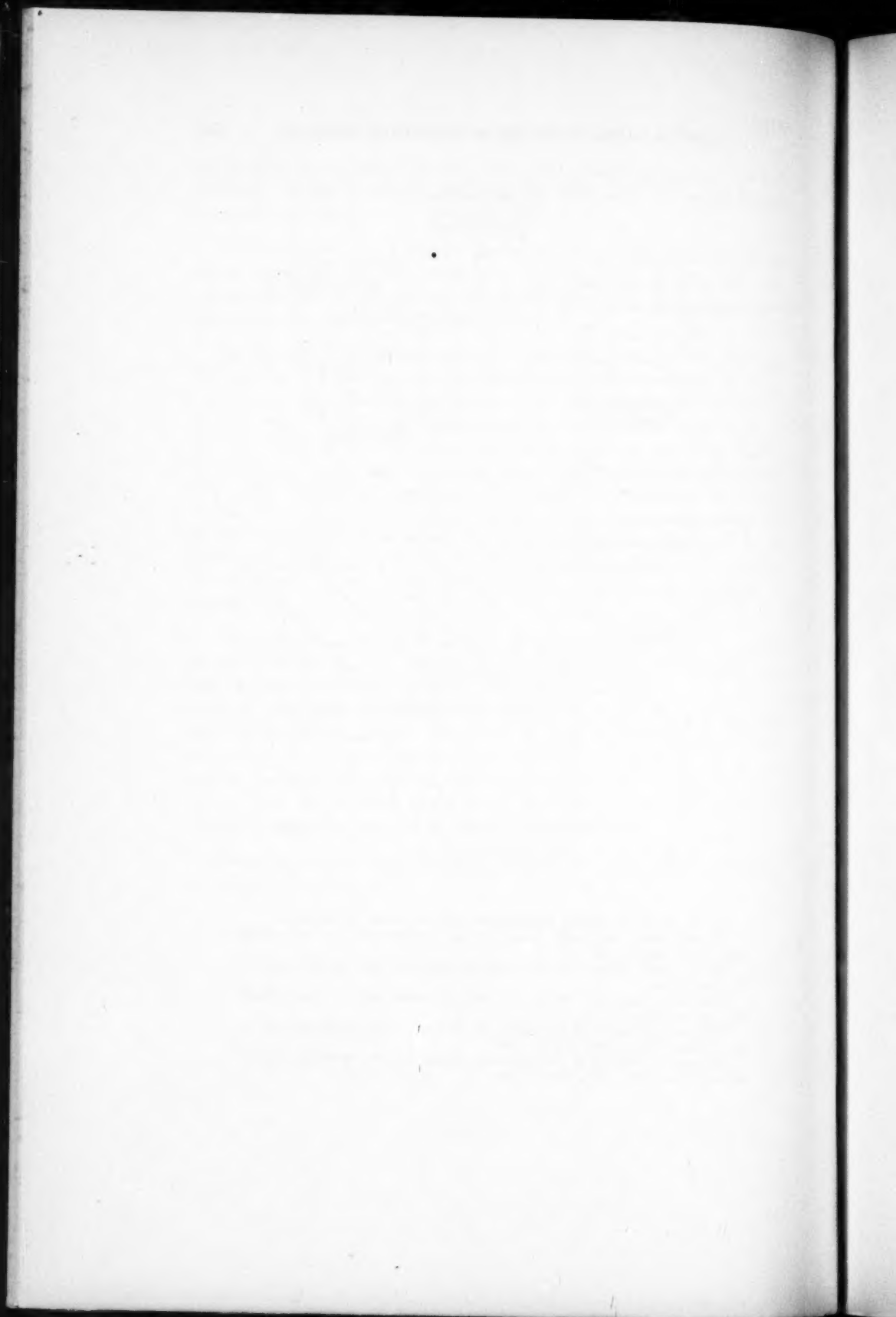
NL—*Nicotiana Langsdorffii*: throat, 1.5 cm.; maximum lobe, .5 cm.; adjacent sinus, .5 cm.; tube, 4 cm.

NA—*N. alata*: throat, 2.5 cm.; maximum lobe, 3.0 cm.; adjacent sinus, 1.1 cm.; tube, 4.9 cm.

NLA—F-1 generation: throat, 2.15 cm.; maximum lobe, 1.4 cm.; adjacent sinus, .9 cm.; tube, 1.9 cm.

NLALA-b—Family b of F-2 generation: throat, 2.1 cm.; maximum lobe, 1.3 cm.; adjacent sinus, .8 cm.; tube, 1.5 cm.

NLALA-g—Family g of F-2 generation: throat, 1.9 cm.; maximum lobe, 1.5 cm.; adjacent sinus, .8 cm.; tube, 1.9 cm.



## RIGHT-ANGLE GRID SYSTEM FOR MAPPING PLANT DISTRIBUTION

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Unless one has a simple, easily executed method for obtaining an exact sample of plant distribution, the problem of mapping large, heavily populated areas is very difficult. At the suggestion of Dr. Lewis F. Thomas, the usual geographic system of right-angle grids was applied to the distribution of *Taraxacum palustre* var. *vulgare*, *T. laevigatum*, and their hybrids in a selected area. This method, as shown below, not only gave an exact record of the numbers and distributions of these plants, but it demonstrated certain phenomena, such as the occurrence of well-defined "neighborhoods" of similar hybrids which had not been apparent from mere inspection. By choosing grids of the appropriate dimensions it should be possible to adapt the method to any particular problem.

The area chosen for mapping was a rectangle, 170 x 30 ft., located on the campus of Washington University, between Rebstock Hall and Forsythe Blvd., which was known from reconnaissance observation to possess quite a dense dandelion population showing evidences of apomixis as well as hybridization. In setting up the grid, wooden pegs were used to indicate the corners and intersections. Strings stretched between them formed the lines, the distance between lines being ten feet. The plants along each line were scored for characters previously selected—leaf shape and seed color—and their positions were recorded. Two hundred and fifty sample leaves fell into five leaf-shape groups, A, B, C, D and E (fig. 1).

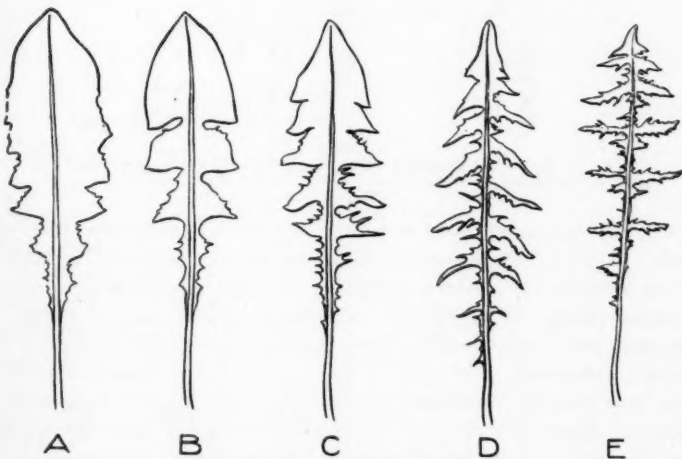


Fig. 1. Types of leaf shape in *Taraxacum*.



The seed types were 1 (gray), 2 (tan), 3 (brown), 4 (pink), and 5 (red). *Taraxacum palustre* var. *vulgare* is characterized by having entire leaves and gray seeds (A-1), while *T. laevigatum* has deeply cut leaves and red seeds (E-5). A map of the grid was drawn to scale. Symbols representing the various features of the dandelions were devised and plotted along each line of the grid (fig. 2 representing a small portion of the map).

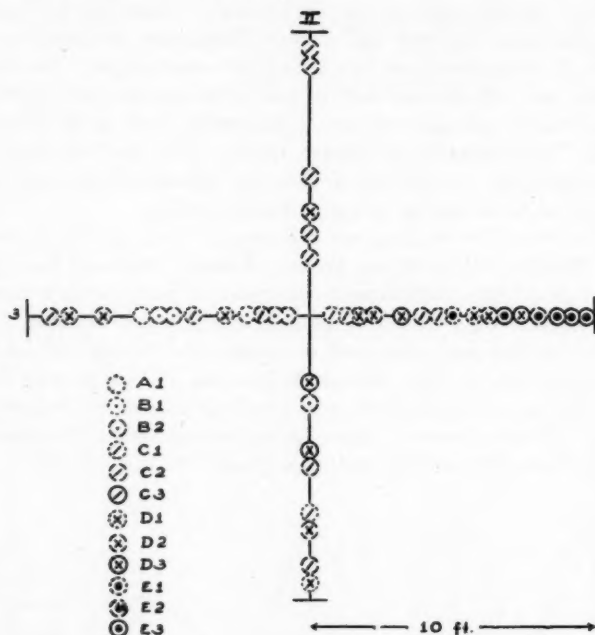


Fig. 2. Individual dandelion plants along Lines II and 3 represented by symbols for leaf shape and seed color.

A simplified map of the total area (fig. 3) indicated certain dandelion "neighborhoods." Plants with dark seeds and deeply cut leaves (similar to *T. laevigatum*) tended to occur in the northern portion of the area; those with gray seeds and entire leaves (similar to *T. palustre* var. *vulgare*) occurred in the southern and eastern part; and the intermediate types with tan seeds and slightly cut leaves were found throughout. The mapping not only made distribution study possible, but also gave data for correlation charts (table I). There is some correlation between leaf shape and seed color, for, although apomixis somewhat clouds the picture, the plants group toward the A-1 (entire leaves, gray seeds) and E-4 (deeply cut, dark) types, rather than the A-4 (entire, dark) and E-1 (deeply cut, gray) types.

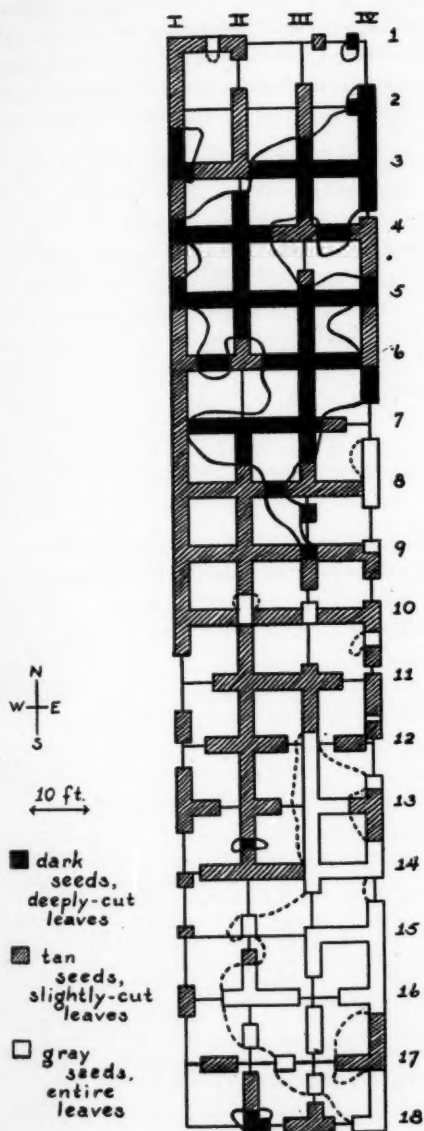


Fig. 3  
Grid map of the total area indicating dandelion "neighborhoods."

The right-angle grid technique has the advantage of being adaptable to any type of plant distribution study, merely by increasing or decreasing the distance between lines. For micro-distribution the scale may be brought down to one yard or one foot; for macro-distribution, one mile or ten miles—whatever distance appears suitable. The traverse map, frequently used in plant distribution study, provides just a linear section, whereas the grid supplies the more complete areal view.

TABLE I  
CORRELATION OF LEAF SHAPE AND SEED COLOR

Number plants along north-south lines						Number plants along east-west lines					
Seed color	Leaf shape					Seed color	Leaf shape				
	A	B	C	D	E		A	B	C	D	E
1	12	21	12	11	2	1	1	6	8	10	5
2	22	96	64	60	16	2		15	30	25	22
3	9	9	18	18	5	3		1	4	10	12
4			1	1		4					1

In conclusion, I wish to thank Dr. Edgar Anderson for his helpful suggestions, Mr. Richard Holm and Mr. Charles Heiser for their assistance in mapping, and especially Dr. Lewis F. Thomas, who proposed this mapping technique.

## A NECTRIA DISEASE OF COFFEE IN WESTERN GUATEMALA<sup>1</sup>

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### INTRODUCTION

Although the *Nectria* canker of *Coffea* probably existed in Guatemala more than a decade ago, little importance was attached to it since only an occasional tree died and had to be removed. In 1935 the trunks of all the coffee trees at La Soledad, a large finca near Tumbador, Depto. de San Marcos, were vigorously rubbed with coffee sacking in order to remove the accumulation of algae, mosses, and lichens. That year the crop production was the highest in the history of the finca, but the following year the *Nectria* canker assumed alarming proportions. This fact suggests that the disease had probably existed before and was spread by the rubbings. It is now to be found in scattered spots throughout the finca.

The study of this disease has been in the direction of a definite determination of its specific causative agent and an attempt to cultivate it artificially and to clarify its relationship to the imperfect *Fusarium* stage.<sup>2</sup>

### THE PERFECT STAGE

The morphological details of the fruiting bodies were studied from a preserved specimen of the diseased bark. To facilitate the identification of the organism, the specimen was embedded according to the method prescribed by Koneff and Lyons<sup>3</sup>. Sections 7.5, 10, and 15  $\mu$  in thickness were made and stained with Heidenhain's iron haematoxylin<sup>4</sup> and safranin.

The organism was discovered to be a species of *Nectria*, a genus which was founded in 1846 by Fries<sup>5</sup> and which was placed in the family Hypocreaceae by Saccardo<sup>6</sup>. It is a genus comprising over 500 species and is divided by Saccardo into ten sections based upon the following characteristics:

<sup>1</sup> An investigation carried out in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Science.

<sup>2</sup> The author wishes to express her appreciation to Dr. C. W. Dodge who, in addition to suggesting and directing the problem, supplied the specimens examined throughout the course of this study and the notes of his field observations. The author also wishes to thank Dr. George T. Moore, Director, for the facilities offered by the Missouri Botanical Garden, members of the Botany department faculty, and members of the library staff, for their assistance.

<sup>3</sup> Koneff, A. A., and W. R. Lyons. Rapid embedding with hot low-viscosity nitrocellulose. *Stain Technol.* 12:57-59. 1937.

<sup>4</sup> Johansen, D. A. *Plant microtechnique*. p. 50. 1940.

<sup>5</sup> Fries, E. *Summa Vegetabilium Scandinaviae*. p. 387. 1846.

<sup>6</sup> Saccardo, P. A. *Sylloge fungorum* 2:479-511. 1883.

- I. EU-NECTRIA—Perithecia typically smooth, caespitose, and with a stroma.
- II. DIALONECTRIA—Perithecia almost separate and smooth.
- III. HYPHONECTRIA—Perithecia smooth but seated upon a cottony subiculum.
- IV. LEPIDONECTRIA—Perithecia scaly.
- V. LASIONECTRIA—Perithecia hairy.
- VI. CRYPHONECTRIA—Perithecia somewhat brittle, almost immersed within a stroma.
- VII. COSMOSPORA—Spores warted, reddish.
- VIII. PHAEONECTRIA<sup>7</sup>—Spores yellow-brown, slightly striate.
- IX. ZIMMERMANIA<sup>8</sup>—Ostiole with a toothed crown.
- X. LICHENONECTRIA<sup>9</sup>—Parasitic upon lichens.

The species, which falls within the section Dialonectria, may be described as follows:

**Nectria Dodgei** Heiser, sp. nov.

Perithecia solitaria vel 2-4 aggregata, 140-270  $\mu$  lata, 160-250  $\mu$  alta, globosa vel ovoidea, laevia, aurantiaca; ostiolum non papillatum; asci ca. 50 x 5  $\mu$ ; ascospores hyalinae, uniseptatae, ellipsoideae, 7.6 x 3  $\mu$ .

Hab: in cortice *Coffea arabicae* var. *maragogipes* vivantis in Guatemala.

Type: in Missouri Botanical Garden.

Perithecia solitary or 2-4 aggregate, 140-270  $\mu$  broad, 160-250  $\mu$  high, globose or ovoid, smooth, orange; perithecial wall pseudoparenchymatous, about 32  $\mu$  thick at the apex and 20  $\mu$  at the base, composed of 3 to 5 layers of cells; cells at the apex very nearly isodiametric, averaging 15 x 17  $\mu$ , cells at the base compressed dorsally, averaging 4 x 13  $\mu$ ; ostiole not papillate, the canal lined with numerous periphyses; asci about 50 x 5  $\mu$ ; ascospores hyaline, uniseptate, ellipsoid, not constricted, 7.6 x 3  $\mu$ .

Hab: On bark of living *Coffea arabica* var. *maragogipes*, in Guatemala.

#### SYMPTOMS

The disease which is produced by *Nectria Dodgei* usually appears under good conditions of culture and manifests itself through the following symptoms:

*Trunk*.—Circular or elliptic cankers occur at the base of the tree and rarely as high as two feet above the soil. Yellow-orange perithecia turning to bright red-brown with age appear on the cankers. The bark becomes blackened, and there is a partial destruction of the tissue which may extend to the cambium. However, below the unfested areas of the trunk the bark is not blackened, and the lateral roots show no rhizomorphs. Sometimes the canker is near an old machete cut, but not enough trees were examined to know whether this is significant or not.

<sup>7</sup> Op. cit. 11:359. 1895.

<sup>8</sup> Op. cit. 17:787. 1905.

<sup>9</sup> Op. cit. 17:797. 1905.



*Roots.*—The blackening on the trunk extends down below the soil and along the tap-root to about one foot below the second laterals. Below that the bark appears normal, nearly white. The wood is normal but the cambium is discolored. The outer layers of bark on the upper laterals show cracking and scaling, with embedded black to dark brown rhizomorphs which change to white as the root becomes smaller; the small rootlets are usually uninfected. The second laterals, being near the lower limits of the blackened bark, show white rhizomorphs near the trunk and little or no infection near the outer ends. Neither the third whorl of laterals nor the lower portion of the tap-root show any infection.

*Leaves.*—The leaves above the canker show irregular mottling at first, as in some mosaics, and then become greenish yellow. They are often spotted like *ojo de gallo*, and tend to fall prematurely.

*Twigs.*—There is frequently some dieback of the twigs as a more or less secondary infection.

*Fruit.*—The fruit is not directly affected. In fact, the last season before the death of the infected side of the tree, a very heavy crop of fruit is set. However, whether or not it matures depends upon the survival of sufficient leaf surface.

#### ISOLATION OF THE FUNGUS

Sabouraud's agar inoculated with the *Nectria* ascospores produced only the imperfect *Fusarium* stage. Numerous attempts were subsequently made to induce the production of the perfect stage on various types of media, but only the repeated production of the *Fusarium* resulted.

Since the *Fusarium* species, in general, show great variability in conidial septation and color reactions under different environmental conditions, the study of the cultural characteristics was restricted to cultures grown only on those types of media used by Reinking and Wollenweber<sup>10</sup> in their work on tropical *Fusaria*. By so doing, the results can be compared more easily with those of the above-mentioned authors, who are among the foremost workers on this difficult group of fungi. The microscopical details were studied from smear mounts (lacto phenol acid fuchsin), hanging drop cultures, and celloidin sections.

#### CULTURAL CHARACTERISTICS

Aerial mycelium white, usually not well developed, smoothly but distinctly warted upon certain media; microconidia<sup>11</sup> straight or allantoid, unicellular, rarely 1-septate, borne in false heads upon simple, occasionally branched conidiophores; macroconidia slightly sickle-shaped, somewhat pedicellate, usually borne in sporodochia; sclerotia and chlamydospores absent. The average measurements of conidia are as follows:

<sup>10</sup> Reinking, O. A., and H. W. Wollenweber. Philippine Jour. Sci. 32:103-253. 1927.

<sup>11</sup> This term is here used to designate 1- and 2-celled conidia.

0-septate	2	x	8.5 $\mu$
1-septate	3	x	14 $\mu$
2-septate	3.5	x	24 $\mu$
3-septate	3.8	x	34.8 $\mu$
4-septate	4	x	41 $\mu$
5-septate	4.5	x	43 $\mu$

The septation of the conidia varies considerably with the type of medium used. For example, on oat agar from 90 to 100 per cent of the conidia are microconidia, but on *Alnus* stems, rice, and potatoes, the number of septa ranges from 0 to 5. Even on these last three, the conidia borne on the mycelium are predominantly 0- to 2-septate, whereas those borne in sporodochia are almost exclusively 3- to 5- (mostly 5-) septate. Although the septation varies greatly with the medium, the size of a particular conidial form is essentially constant; that is, unicellular conidia from Substrate A will have approximately the same dimensions as those from Substrate B even though they may be present in greatly different percentages upon the two media.

The following observations were all made of cultures one month old:

*Hard potato agar*.—Cultures characterized by a medium growth of white to pale pinkish buff<sup>12</sup> woolly mycelium, often with a dull blackish green line in the agar along the line of inoculation, and a raw sienna ring around the base. A cream buff and water green pionnotal mass may be present.

*Potato-agar plate, 5 per cent dextrose*.—Rather scant, woolly, loosely matted, grayish white aerial mycelium produced over the plate, the agar becoming citrine or vetiver green and sometimes grayish blue green in part.

*Oat agar*.—Fine cottony pinkish buff mycelium produced at the tip of the slant; the rest of the slant showing little aerial mycelium and being rather powdery in appearance. The agar appears much the same as on the potato-agar plates, and is dark Delft blue near the base.

*Rice*.—Fine cottony white mycelium produced on top of the medium; mycelium at bottom of the tube light grayish vineaceous. Color of the rice ranges from white through sayal, pecan, and wood brown to liver brown. Heaps of light ochraceous buff pionnotes, which become almost black with age, appear throughout the rice. No benzoic odor noticed.

*Potato-tuber plug*.—Cultures characterized by white to cinnamon buff felty mycelium that may be honey yellow, forest green, deep grayish olive, and dark Delft blue in patches. Sporodochia may or may not be present.

*Alnus stem*.—A tuft of fine white mycelium occurs at the point of inoculation, the growth being rather scarce over the remainder of the stem. A number of white and tawny sporodochia are present on the lower portion.

<sup>12</sup> All color terms mentioned in this section are according to: Ridgway, R. Color standards and color nomenclature. 1912.

In addition to the various media mentioned in the preceding paragraphs, a number of others were also inoculated, with the primary object of promoting the growth of the *Nectria* stage. Although in no instance was the *Nectria* produced, some supplementary observations were able to be made concerning the growth of the imperfect stage. Prune agar, coffee-dextrose agar, and potato-dextrose agar (with and without 1 per cent glycerin) all produced much more abundant mycelial growth than any of the media mentioned heretofore. Growth was rather sparse upon Sabouraud's agar and coffee agar, and practically nil upon corn-meal agar. Autoclaved coffee twigs (in a tube having one inch of glass wool covered with 1 per cent glycerin) produced a medium amount of mycelial growth and sporodochia at the base.

Upon prune agar and Sabouraud's agar the mycelium had rather rounded warts, a character not apparent on the other media.

Since several different isolations were made from the diseased coffee trees, cross-inoculations were made upon autoclaved coffee twigs, Sabouraud's, and potato-dextrose agar plus 1 per cent glycerin, in an attempt to discover possible existence of different physiological strains. Here again the results were negative.

#### COMPARISON WITH OTHER NECTRIAS DESCRIBED ON COFFEA

In order to show how *N. Dodgei* differs from the other species of *Nectria* described as growing on *Coffea*, a key based upon morphological differences, followed by a discussion of physiological differences, is given:<sup>13</sup>

- I. Perithecia yellow and clothed with well-developed hairs..... *N. luteopilosa*
- II. Perithecia not clothed with well-developed hairs.
  - A. Perithecia reddish brown.
    - B. Perithecia caespitose or subcongested; spores sub-fusiform..... (*N. saccharina*)
    - BB. Perithecia densely gregarious; spores ellipsoid..... (*N. coffeicola*)
  - AA. Perithecia yellow, orange, red, or purple.
    - B. Spores less than 10  $\mu$  long..... *N. Dodgei*
    - BB. Spores more than 10  $\mu$  long.
      - C. Perithecia over 250  $\mu$  in diameter.
        - D. Spores ellipsoid or fusoid, 14-15  $\mu$  long..... (*N. anisophila*)
        - DD. Spores ovoid, 8-12  $\mu$  long..... *N. tropica*
      - CC. Perithecia less than 250  $\mu$  in diameter.
        - D. Spores 17-20  $\mu$  long..... (*N. coccidophthora*)
        - DD. Spores 10-13  $\mu$  long.
          - E. Spores constricted.
            - F. Perithecia sparse to sub-aggregate, red..... (*N. Behnickiana*)
            - FF. Perithecia densely aggregate, yellow..... *N. fructicola*
            - EE. Spores not constricted..... *N. coffeigena*

Of the ten species listed in the key one has subsequently been transferred to another species of *Nectria*, and four have been transferred to the genus *Hypomyces*. This is readily understandable since the two genera are closely related. Both are in the Hyalodidymae section of the Hypocreaceae, the chief difference being that

<sup>13</sup> *Nectria coccidophthora* has been transferred to *N. coccophila*, and the other species enclosed in parentheses have been transferred to the genus *Hypomyces* by Wollenweber (in Reinking, O. A. and H. W. Wollenweber, Die Fusarien. pp. 34, 132-133, and 159. 1935).

the perithecia of *Hypomyces* are somewhat immersed while those of *Nectria* are more or less superficial.

Probably only four of the species are parasitic on *Coffea*. The remaining six are most likely only saprophytic since they were described from dead leaves, twigs, and fruit, and no indication was given in the original descriptions that they were the cause of any diseases. In addition, none of them has since been reported as the cause of any disease of *Coffea*.

Although *Hypomyces ipomeae* (*N. coffeicola*)<sup>14</sup> was found on stumps of dying coffee trees, it is doubtful if that fungus was the cause of death because: (1) no mycelium was found in the cambium; (2) the species was also reported on *Melia Azedarach* and dead fruits of *Theobroma Cacao*; and (3) wound inoculations of living trees failed to give positive results. *Nectria luteopilosa* and *N. fruticicola*<sup>15</sup> were both found on blackened fruits of *C. liberica* in Java. *Hypomyces ipomeae* (*N. saccharina*),<sup>16</sup> *H. ipomeae* var. *major* (*N. Bebnickiana*),<sup>17</sup> and *N. coccophila* (*N. coccidophthora*)<sup>18</sup> were found on dead coffee twigs, the last two being reported upon hosts among other genera also.

The chief problem lies, then, in distinguishing *Nectria Dodgei* from *N. tropica*,<sup>19</sup> *H. baematococcus* (*N. anisophila*),<sup>20</sup> and *N. coffeigena*,<sup>21</sup> all of which cause diseases of *Coffea*. In addition to the differences in morphological details indicated above, these four organisms may also be distinguished on the basis of their pathological effects upon the host.

The disease caused by *N. coffeigena* is characterized by cankers localized principally at the top of the trunk as contrasted with the basal cankers of *N. Dodgei*. The disease caused by *H. baematococcus* (*N. anisophila*) was reported from Costa Rica, and although some of the symptoms it produces overlap those produced by *N. Dodgei*, such as blackening of the stem, defoliation, and failure of the fruit to mature, there are several important differences. In *H. baematococcus* (*N. anisophila*) a large number of rootlets become blackened and partially or totally necrotic and "often the injury extends to the primary and secondary roots."<sup>22</sup> In *N. Dodgei* the root infection is mainly on the first and second laterals and upper portion of the tap-root, while the small rootlets usually remain uninfected. Also the blackening occurs on the basal portion of the trunk below the canker, whereas in *H. baematococcus* it is the young shoots which become blackened.

The other organism which must be distinguished from *N. Dodgei* is *N. tropica*.

<sup>14</sup> Zimmerman, A. Centralbl. für Bakt. II, 7:101-106. 1901.

<sup>15</sup> *Ibid.* 8:182. 1902.

<sup>16</sup> Berkeley, M. J., and M. A. Curtis. Jour. Linn. Soc. Bot. 10:174. 1869.

<sup>17</sup> Hennings, P. Hedwigia 44:172. 1905.

<sup>18</sup> Zimmerman, A. Centralbl. für Bakt. II, 7:872. 1901.

<sup>19</sup> Toro, R. A. Phytopath. 19:969-970. 1929.

<sup>20</sup> Picado T., C. Jour. Dept. Agric. Puerto Rico 16:389-400. 1932.

<sup>21</sup> Pascalet, M. Ann. Cryptogam. Exot. 7:21-22. 1934.

<sup>22</sup> Picado T., C. *op. cit.*

It was originally described as *N. coccinea* var. *tropica* by Wollenweber<sup>23</sup> from Brazilian coffee collections and later was given specific rank by Toro,<sup>24</sup> who reported it from Colombia. His basis for giving it specific rank was the "contextu radiati-fibrato peritheciolorum" character which was entirely wanting in *N. coccinea*. In addition, the spores were much smaller than in *N. coccinea*. This organism causes a disease known under the common name of "llaga" (canker). Toro reports that there are two distinct sets of symptoms. The one is characterized by a dry rot on the upper surface of the roots and the base of the trunk. The bark turns black and partially disintegrates, thus exposing the wood. In the second form, which is said to be rarer, the bark often remains attached and acquires a greenish color. Sometimes it turns soft and gives off a pungent odor. In a few cases the perithecia of *N. tropica* were found on the roots and stumps of coffee trees which had died from this second form. The connection of these two sets of symptoms with the same disease was established upon the fact that in some cases of the second form "the mycelial strands of the first form were also present."<sup>25</sup>

According to Alvarado,<sup>26</sup> who reported the same disease from Guatemala, the canker is more or less extensive over the shoots and roots, and after the death of the tree the fungus forms a single gangrene covering the whole tap-root. From the fact that the fungus gains entrance to the roots through wounds, he concludes that insect wounds and careless cultural practices are predisposing factors of the disease.

*Nectria Dodgei*, in contrast with *N. tropica*, causes a canker of much more limited extent, and there is no such characteristic gangrene in connection with which the perithecia of *N. tropica* are produced. Furthermore, there is some evidence to indicate that *N. Dodgei* is wind-disseminated, because the infected trees seem to form a linear pattern which corresponds to the direction of the prevailing winds. At the same time, evidence shows that *N. Dodgei* is not spread through the soil, since when clods of soil adhering to an infected stem and upper lateral were carefully scraped off and examined with a hand lens no rhizomorphs were found.

Judging from the three accounts of *N. tropica*, some confusion seems to exist as to the conidial stage, thus raising the question of whether the authors were dealing with the same organism. As Wollenweber<sup>27</sup> described the fungus, the conidia were 5-7-septate. Toro,<sup>28</sup> who reported a *Fusarium* associated with his specimen of *N. tropica* (although the relationship was not proved), could very well have been dealing with the same organism. Alvarado,<sup>29</sup> while apparently dealing with the same organism on the basis of pathological effects upon the host,

<sup>23</sup> Wollenweber, H. W. *Angew. Bot.* 8:191. 1926.

<sup>24</sup> Toro, R. A. *op. cit.*

<sup>25</sup> *Ibid.*

<sup>26</sup> Alvarado, J. A. *Tratado de caficultura practica.* 1:319-320. 1935.

<sup>27</sup> Wollenweber, H. W. *op. cit.*

<sup>28</sup> Toro, R. A. *op. cit.*

<sup>29</sup> Alvarado, J. A. *op. cit.*



states quite definitely that the conidial stage is *Tubercularia vulgaris*. Since *T. vulgaris* is classed among the Amerosporae, it cannot possibly agree with the conidial stage described by Wollenweber. In spite of the fact that Toro and Alvarado may have been dealing with different organisms, either organism in question may be distinguished from *N. Dodgei* on a pathological basis. Furthermore, Toro's account, which deals with the morphological as well as the physiological aspect, shows that *N. tropica* can be distinguished from *N. Dodgei* on a morphological basis alone, by its much larger perithecium, 380–450  $\mu$ , its purple color, and its "contextu radiati-fibrato perithecorum."<sup>30</sup>

#### CONTROL MEASURES

In April part of the coffee tree trunks at La Soledad were painted to a height of three feet with lime sulphur or a type of Bordeaux mixture. By the end of May, except in a few cases where normal perithecia were found in the crevices, which evidently had not been completely covered by the brush, the "Bordinette" was effective. It also killed most of the algae, mosses, and lichens except a species of *Isidium* which remained healthy-looking. Lime sulphur appeared more efficient, however, in the control of both parasite and epiphyte, since it killed everything except *Isidium* and that looked quite sick.

#### INOCULATION OF COFFEE PLANTS

On March 11, 1944, in the Washington University greenhouse, three 3- to 5-year-old plants of *C. arabica* were inoculated with a spore suspension of a 5-day-old potato-dextrose agar culture of the *Fusarium*. Three plants of *C. excelsa* were also inoculated, and a control was kept of each species. One plant of both species was sprayed in an attempt to learn if the organisms were able to penetrate uninjured tissue; one of each was wound-inoculated near the base of the stem; and the soil in the flower pots containing the remaining two plants was inoculated to learn if the organisms could gain entrance through the roots. After a lapse of one year none of the symptoms characteristic of the disease appeared in any of the plants, but the negative results cannot be accepted as conclusive until the experiment is repeated and revised in such a manner as to eliminate the following possible causes of failure: (1) The only plants available for inoculation were not of the same variety as the ones from which the disease was described and were probably more resistant. (2) Some factor in the environment may have made the test plants more resistant to infection, although every attempt was made to simulate as closely as possible the natural environment of the coffee plants. (3) The prolonged period of culture upon artificial media may very likely have resulted in the loss of virulence of the *Nectria*. (4) The age of the coffee plants tested may also have been a factor in their increased resistance over older plants.

<sup>30</sup> Toro, R. A. *Phytopath.* 19:969-970. 1929.



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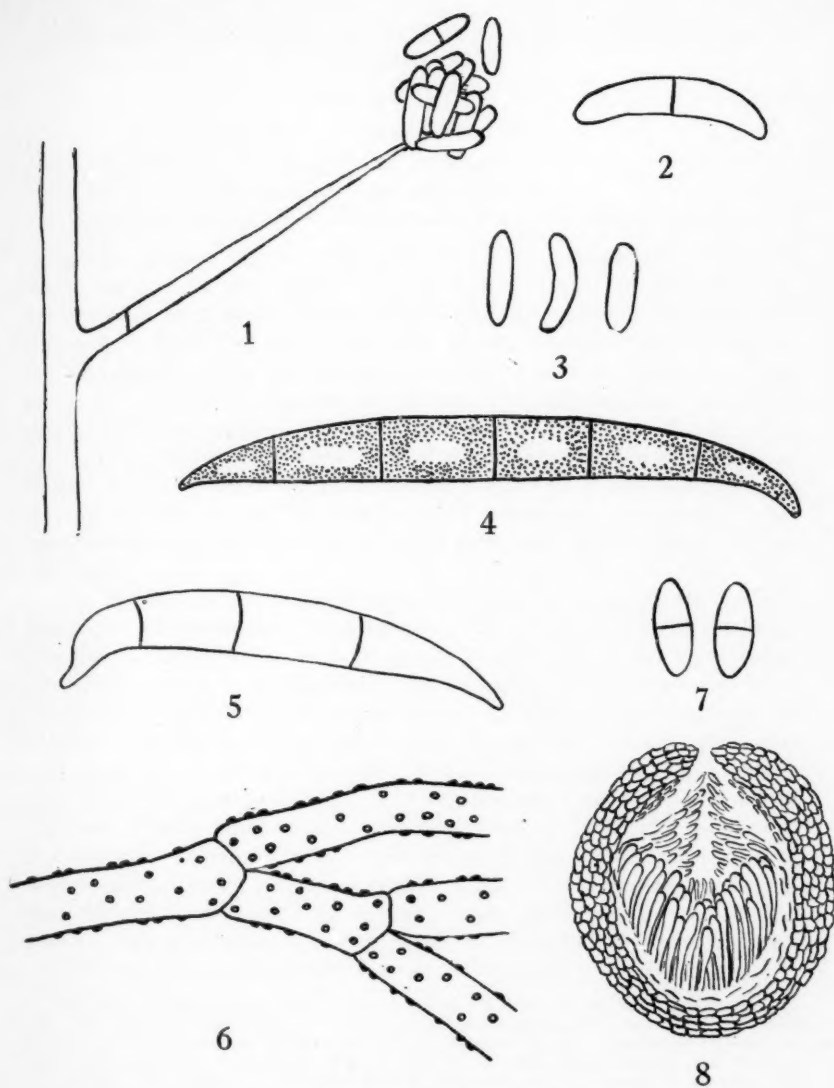
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## EXPLANATION OF PLATE

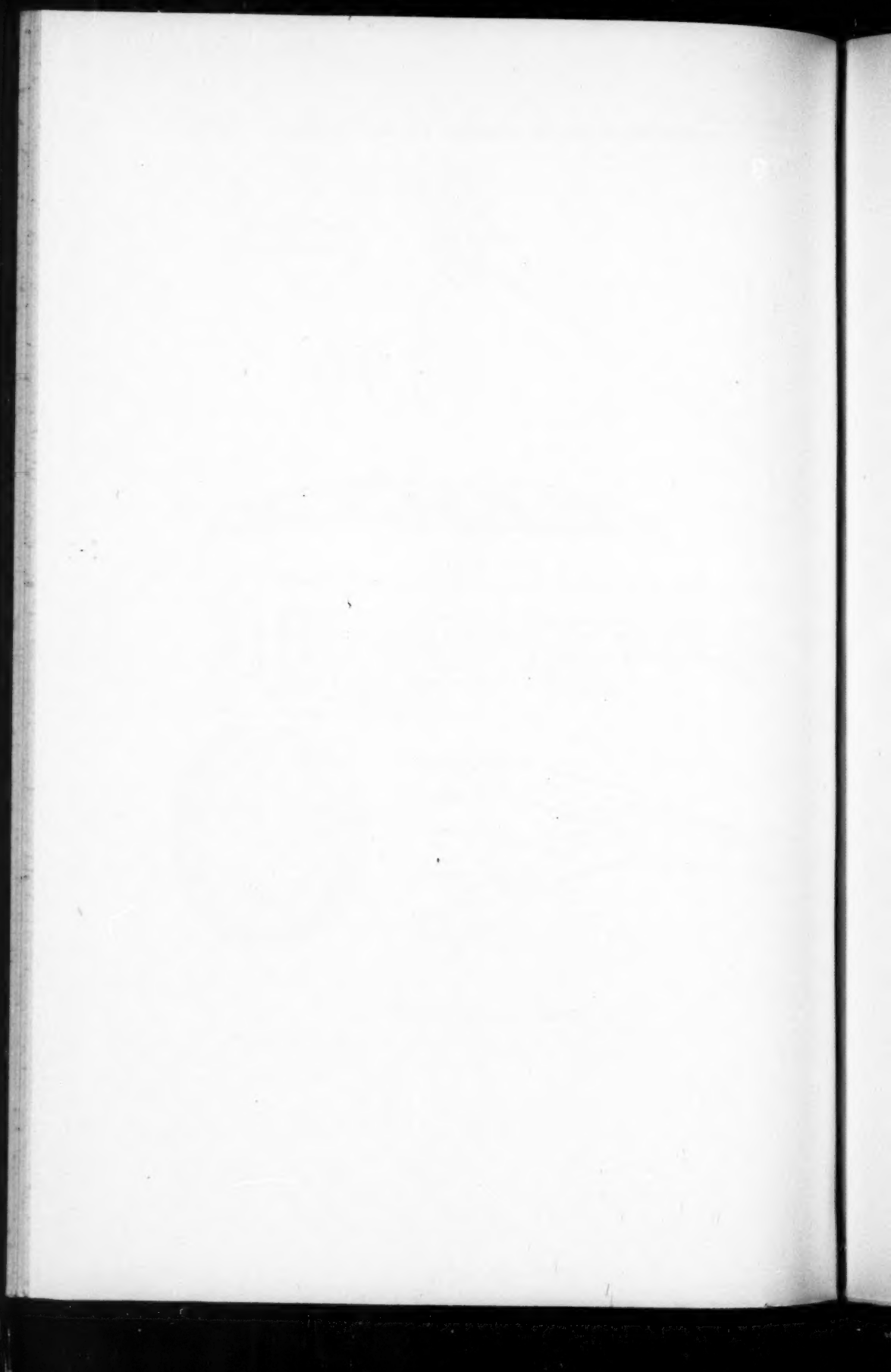
## PLATE I

*Nectria Dodgei*

- Fig. 1. Microconidia borne in a false head, from a 6-day Sabouraud's agar culture, X 755.
- Fig. 2. Two-celled microconidium from a 30-day potato-plug culture, X 1620.
- Fig. 3. Unicellular microconidia from a 30-day oat agar culture, X 1320.
- Fig. 4. Six-celled macroconidium from a 21-day hard potato-agar culture, X 1500.
- Fig. 5. Four-celled macroconidium from a 30-day potato-plug culture, X 1500.
- Fig. 6. Warty mycelium from a 7-day prune-agar culture, X 1580.
- Fig. 7. Ascospores, X 1500.
- Fig. 8. Perithecium, X 175.



HEISER—NECTRIA DODGEI



## A PRELIMINARY SURVEY OF MAIZE IN THE SOUTHWESTERN UNITED STATES<sup>1</sup>

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Maize is uniquely variable; differences from plant to plant, from variety to variety, and from region to region are even greater than in other cultivated plants. Previous papers by Anderson and his collaborators (Anderson and Blanchard, '42; Anderson and Cutler, '42; Kelly and Anderson, '43; Anderson, '43a, b, '44a, b) have discussed the means of cataloguing this variation most effectively. They have recorded it in detail, character by character, and have described a few of the races and sub-races which are already apparent in our collections. The following paper is an attempt to classify the maize of the southwestern United States, particularly the varieties grown by the Indians. While it is more comprehensive than any previous attempt, we consider this a preliminary report since it raises many more questions than it answers, and of these, many should yield to further investigation.

Maize is also unique for purely technical reasons in its excellence for both cytogenetic and archaeological investigation. For cytogenetics it has the initial advantages of many readily available unit characters such as starchy vs. sweet kernels; green leaves vs. purple leaves. For cytological analysis it has the advantage of long, well-differentiated chromosomes. To these original advantages has been added by cooperative research a wealth of detailed technical information unparalleled for any other plant (see Rhoades and McClintock, '35). Archaeologically, maize has the advantage of its large indurated ear which resists decay and which presents almost as many significant characters for racial diagnosis as does the human skull. Therefore, when cytogenetic and archaeological informations are merged we may expect eventually a more complete, detailed, and significant history than is possible for any other cultivated plant or any domesticated animal. Such a synthesis would be useful to geneticists, archaeologists, corn breeders, geographers, ethnologists, and culture historians.

<sup>1</sup> This paper results from the active collaboration of a number of individuals and institutions. The actual funds were supplied by University of California, Guggenheim Foundation, Penrose Fund of the American Philosophical Society, and Missouri Botanical Garden. Laboratory facilities and garden space have been provided by Missouri Botanical Garden, Blandy Experimental Farm of the University of Virginia, Cold Spring Harbor Laboratory of the Carnegie Institution, and California Institution of Technology. Grateful acknowledgment is made to these institutions, as well as to the following individuals: Hugh C. Cutler, E. G. Anderson, A. L. Kroeber, Carl Sauer, E. W. Gifford, Paul C. Mangelsdorf, Barbara McClintock, Volney Jones, O. E. White, Marcus M. Rhoades, Merle T. Jenkins, R. C. Reeves, George F. Will, F. W. Hodges, H. S. Cotton, Emil Haury, and A. F. Whiting.

For a number of reasons the classification of southwestern maize is a relatively simple problem; simple, that is, by comparison with modern commercial maize or the maize of Central America or of South America. Since the beginnings of its agriculture the Southwest has been semi-isolated from other agriculturally developed areas by geographical and climatic factors, and interchange with other areas has been comparatively slight. Within the region itself, maize growing has been strongly localized by climatic conditions; i. e., in contrast to Mexico or Guatemala fields were few and far apart, giving opportunity for the development of well-differentiated local varieties. Compared to most areas, the Southwest is well known ethnologically and archaeologically. Modern and prehistoric maize is already on hand in museum collections<sup>2</sup> in considerable quantity while in practically any other area one must first assemble his own collections. We have artificially simplified the problem even further by leaving out the question of sweet corn. It is grown by a number of southwestern tribes (most particularly by the Hopi), but as Kelly and Anderson have pointed out ('43), the origin of sweet corn is a rather different problem technically from the origin and development of dent and flour corns. The whole question of sweet corn in the Southwest is therefore postponed for further publication.

Unfortunately, collections of modern maize need to be made with extreme care if they are to be of maximum usefulness. Maize is a very sensitive mirror of the people who have been growing it. Collections made from Indians living along concrete highways or in the suburbs of modern American towns will be faithful reflections of the extent to which they have left their old ways. A progressive Papago Indian who owns a small truck and lives on the highway between Sells and Tucson will have seen various kinds of maize in the course of his work and may bring back a good many to try out in his corn field. While most of them may not be well suited to these peculiar desert conditions, if they survive even for one season, the wind may carry their pollen to other plants and a new element will have been introduced into this particular cornfield. Yet the ordinary collector will be satisfied with Papago maize from such a source and will not press on over the long dry road to Sells and then go farther still on side roads into the reservation to find Papago maize which shows no evidence of Yankee contact, none of Spanish contact, and very little contact with other Indians. Yet such maize was characteristic of Papago communities as late as 1943. To some students who have collected maize in the Southwest an Indian was an Indian, and the idea of spending an extra day or an extra week in reaching a seed source of unimpeachable significance seemed a waste of time and effort in a country where travel was difficult. Even those who understood these matters were impeded by the practical necessity of getting back to their base of supplies. The very slight literature on the maize of the southwestern Indians is therefore shot through with information which is only partly true and which would need the joint services of an agronomist and an ethnologist to interpret correctly.

<sup>2</sup> As, for instance, the remarkable collection assembled by Volney Jones and A. F. Whiting at the Museum of Northern Arizona (See Whiting, '39).



In so far as possible our collections were made directly from Indian fields or granaries and from Indians who by ethnological standards were representative members of their groups. The numbers of ears are small (Table II) but the collections are more significant than larger, uncritical ones. Since much of the work was done while both of the authors were traveling from place to place it was seldom possible to measure the entire collection (the bulk of which was divided between Berkeley and St. Louis). Accordingly, for most of the pueblos, the quantitative observations reported below have been confirmed by qualitative observations on a duplicate collection. More recently the junior author has had the opportunity to measure comprehensive collections of twenty-five ears each for eight different varieties. These were distributed as follows: Papago, Tesuque, San Juan, Navajo, Hopi (two varieties), Isleta (two varieties). All these collections confirm and extend the conclusions reached in this paper.

One's first impression of the maize grown in most of the pueblos is that it is extremely variable. This is due to the fact that the eye is quicker to note differences in color than in proportion. Color differences, however, are relatively superficial. In the entire Southwest not more than ten loci in the germ-plasm are responsible for the variation in cob and kernel color, while many more than that are at work in determining cob shape, kernel size, row number, etc. As explained in the first paper in this series (Anderson and Cutler, '42), such characters, though difficult to work with, are therefore superior as criteria for races and sub-races. Color differences, however, have not been ignored but were the object of a special investigation which will be published separately.

One of the characters used in our classification deserves special discussion, partly because it is so important in revealing differences and resemblances between southwestern varieties and partly because its exterior manifestations are somewhat different in the Southwest from what they are in other regions. This character is technically known as denting. In its typical form (pl. 3) it produces a mature kernel which is shrunken at the tip. It is, however, an extremely variable character, and the dent may be either rough or smooth and deep or shallow. When well developed it will affect all the kernels on the ear with the possible exception of a few at the base and the tip. Genetically, we know very little about this character except that it is complex and is apparently affected by a very large number of genes. Our collections of North American maize show that denting reached its strongest development in the region around Mexico City and radiates from there in all directions. In the Southwest it is present but in a very diluted state. Many of the ears which we have scored as dented (pl. 3) would not be referred to as dent corn in the American corn belt, but upon careful examination several of the kernels show a slight dent in the surface of the kernel. Examination of granaries and maize fields have shown us that when such ears are found, invariably sister plants occur with kernels much more strongly dented. Archaeologically, denting is important because it indicates some kind of connection with the Mexican Plateau and because it is one of the consistent differences between

Pima-Papago and Basketmaker maize. When and by what route it entered the Southwest is a matter of great archaeological importance. Collections of prehistoric maize in the Southwest should be carefully examined for any indications of dented kernels. They are illustrated, though without comment, in Nussbaum and Judd's collections from Cottonwood Cañon in southeastern Utah, and the remarkable ears collected by Scoggin in northwestern Colorado (which were submitted to us for study) are as strongly dented as Mexican varieties.

Maize in the Southwest stems from at least four different sources. (1) The race grown by the prehistoric "Basketmakers," the first agriculturists of whom we have any record in the area, was relatively uniform. It was slender-cobbed, tessellate-seeded (like tiles in a pavement, see pl. 2), compressed at the butt, and with strong husk striations. Unfortunately, not enough plant material has been saved in archaeological studies to indicate the plant type associated with this type of ear. (2) Similar (though apparently not identical) varieties are still being grown by the Pima, the Papago, the Yuma and related tribes. They too are slender-cobbed, tessellate-seeded, and striated. The plants of these modern varieties are slender-stalked and narrow-leaved and have tillers which are sub-equal to the main stalk.

The maize of the Pueblo Indians shows strong influence from at least two other strains. It would be out of place in this preliminary discussion to go into the complex problem of just where and when the modifications took place. The old types were not completely replaced, for most of the Indian maize of the Southwest has a very strong resemblance to Basketmaker corn (as will be demonstrated below). Regardless of source, the two later introductions brought in characters which are identified with two other regions. (3) Condensed tassels (Anderson, '44b), denting of the kernel, weak leaves, a strongly tapered ear, and high row number are characteristic of the maize of the Mexican plateau. (4) Present as an admixture in Pueblo corn is a complex of characters which in its most extreme form is apparently limited to Guatemala. It is, however, markedly present in the flint and flour corns of the eastern United States though absent from most of Mexico. It is characterized by strong, arching leaves, coarse stalks, a large indurated shank below the ear, and an ear whose butt end is perceptibly larger than the rest of the kernel-bearing portion. The kernels are wide, often wider than they are long, and are arranged in long, straight, regular rows, aside from the base of the cob where the rowing is usually irregular. Throughout the remainder of this paper these last two complexes will be referred to as "Mexican" and "Eastern." These names are chosen for convenience and the two complexes may have come into the region separately or together. It is even possible that the one we are calling "Mexican" may have entered from the Northern Periphery.

If we postpone the historical interpretation of these complexes and merely use them as cataloguing devices, the results are suggestive. Figure 1 shows the data on a Mexican character (denting) and an Eastern character (wide kernel) set out in the form of a scatter diagram. A similar, but by no means identical, diagram

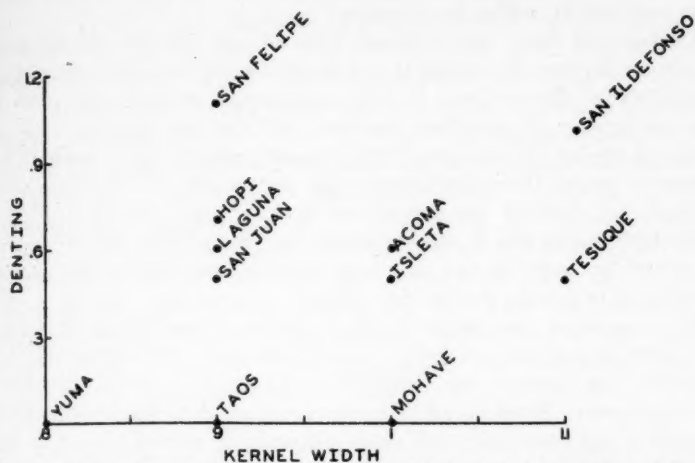


Fig. 1. Scatter diagram showing the relationship between the varieties of maize grown by various tribes in the Southwest. Each dot is an average of all the collections from the tribe.

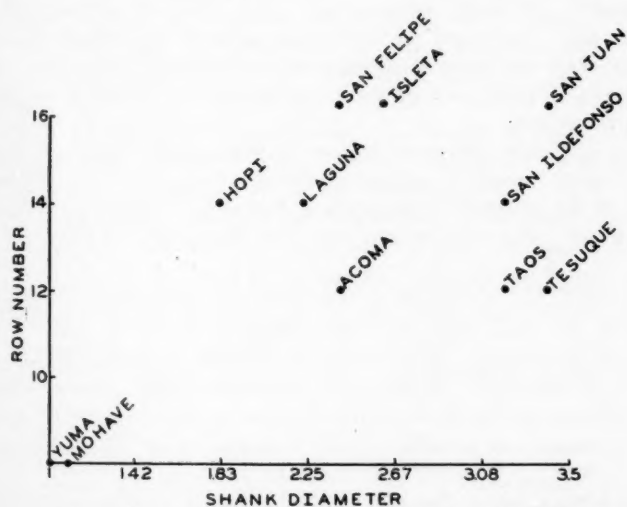


Fig. 2. The same collections as diagrammed in fig. 1, but using two different characters. In both figures a "Mexican" character has been used on the vertical axis, and an "Eastern" character on the horizontal axis.

(fig. 2) is produced if we choose two other characters, taking row number from the Mexican complex and shank diameter from the Eastern. In figs. 1 and 2 all the ears of maize from each group of Indians have been averaged and the average

values were used in making the diagrams.

The fact that figs. 1 and 2, though based on very different criteria, produce such similar diagrams of relationship, is evidence for the validity of the complexes described above. It is evidence that the combinations of characters which tend to be seen together are not wholly fortuitous and that their resemblance to races of maize in Mexico and in eastern North America probably has an historical basis. In terms of genetics it probably means that row number and denting are both multiple factor characters and that, though there has been a great deal of crossing of different types of corn in the Southwest, high row number and denting went into the mixture together (we now have archaeological evidence for this fact) and still tend to stay together on the average.

The existence of these loosely linked complexes of characters in southwestern maize allows us to extend a technique originally developed for dealing with hybrid populations (see Anderson and Turrill ('38) for details). In practice this was done step by step. When the two diagrams (figs. 1 and 2) were averaged mathematically it was found that while either one produced a fairly natural classification of the tribes and one that was in harmony with what was known about the history of their agricultural relationships, the combination of the two was superior to either alone. Row number and denting were used together as an index of the Mexican complex, and shank diameter and kernel width as an index of the "Eastern" complex. Additional characters were added to the indices, one at a time, until at length the ten most objective and easily scored criteria were being combined in each diagram, each of the characters being given equal weight in constructing the indices.

All of the qualitative characters are put in three grades, "present", "intermediate" or "absent," which are assigned numerical values of 2, 1, and 0, respectively. Each of the quantitative characters is divided into three classes, likewise scored from 0 to 2. The actual scoring for all ten characters is as follows:

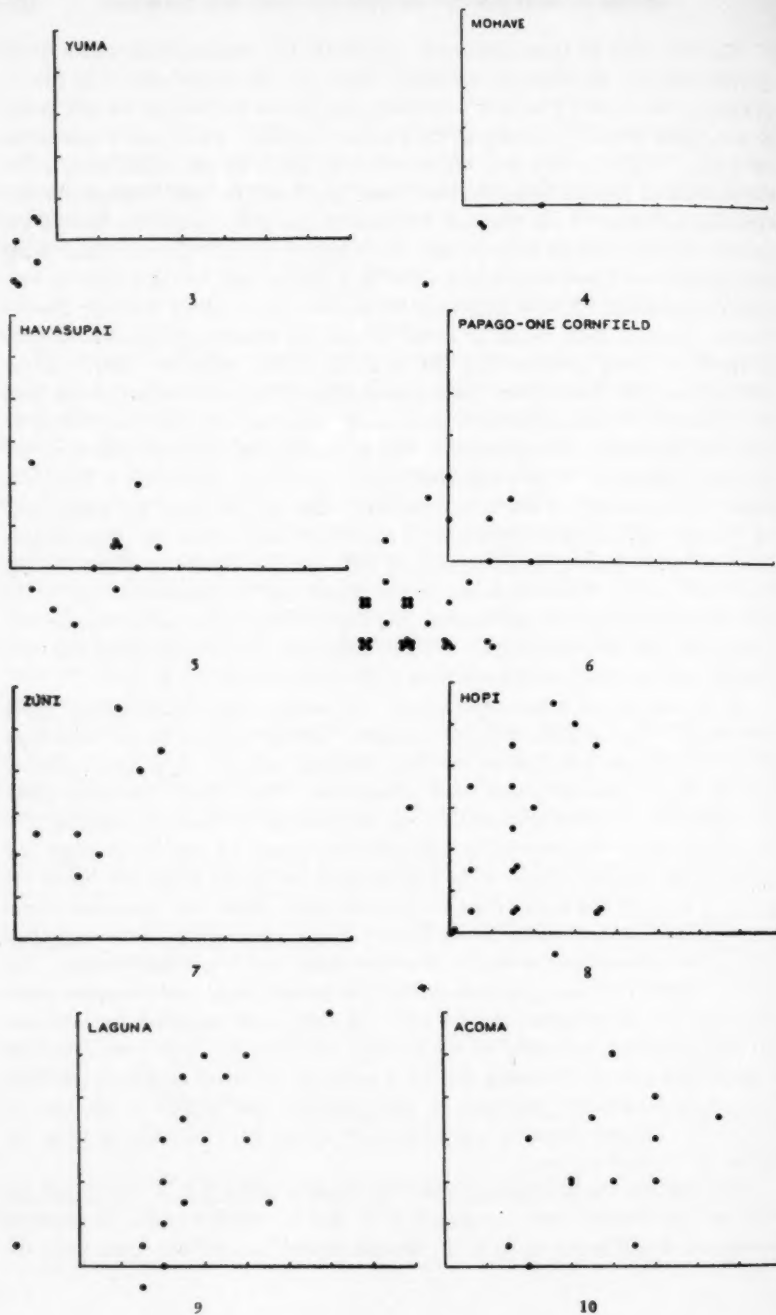
TABLE I

		0	1	2
"Mexican"	Ear taper High row number Denting	None 8-12 None	Slight 14 Slight or variable	Well-marked 16 or more Uniform or deep
"Eastern"	Enlarged butt Straight rows, uniform kernels Wide kernels Wide shank diameter	None None to .9 cm. to .9 cm.	Slight Moderate 1.0 cm. 2.0-2.6 cm.	Strongly developed Kernels very uniform 1.1 cm. or more 2.7 cm. or more
Non-Mexican Non-Eastern	Mid-ear diameter Husk striation Basal compression of ear	to 4 cm. None None	4.1-4.3 cm. Slight or variable	4.4 cm. or more Strongly developed Strongly developed

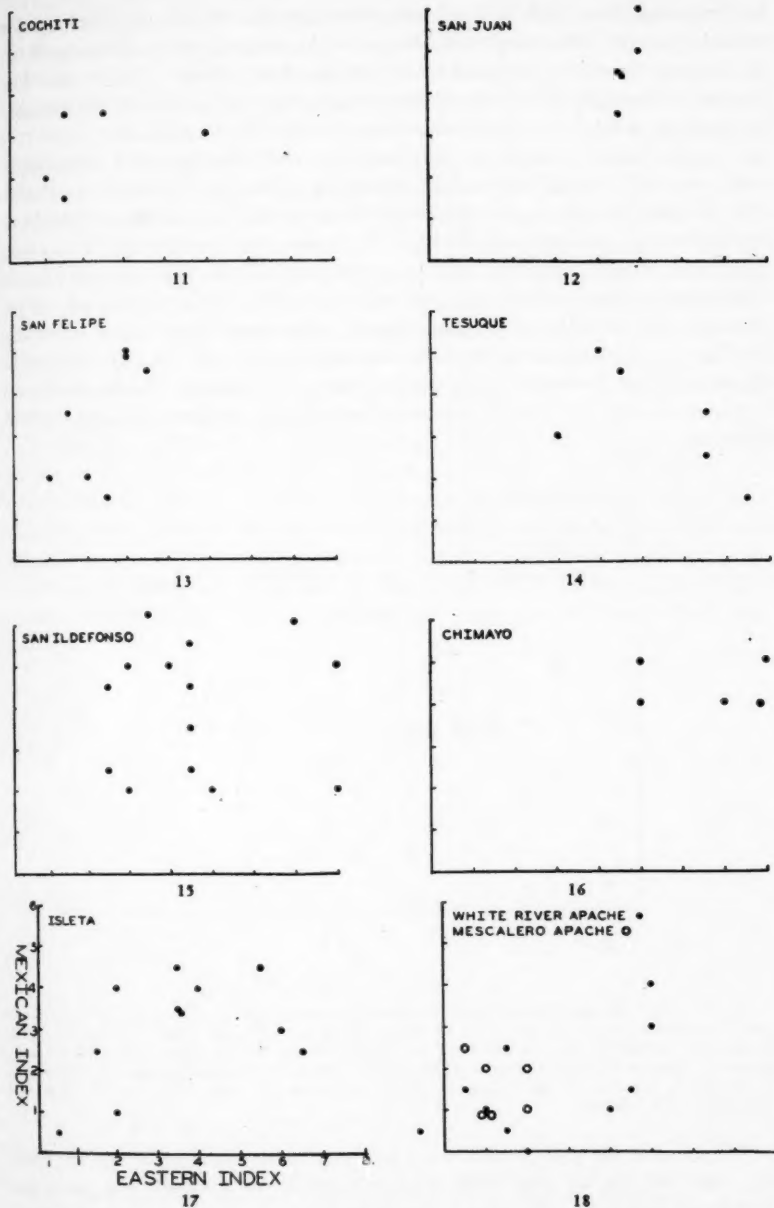
The first three of these characters (ear taper, row number, and denting) are characteristic of the Mexican complex. They are all added and their sum is plotted on the y axis. The next four (enlarged base of ear, regular kernels, width of row, shank diameter) belong to the Eastern complex. Their sum is plotted on the x axis. We come now to a cluster of traits which do not characterize either the Mexican or Eastern complexes but which are found in both Basketmaker and Pima-Papago maize: a narrow cob, longitudinal striations across the face of the kernels, and basal compression of the ear. Depending upon the way these traits were defined and scored they might either be added to each of the indices or subtracted from each. If husk striations, for instance, were scored for their absence then the resulting score would be *added* to both the Eastern and Mexican indices. If scored for their presence then the resulting values would be subtracted for both indices. We found that for rapid scoring of large collections errors were apt to creep in if some characters were being scored in a negative and others in a positive direction. Accordingly, in taking the original data we scored all the characters positively. This complicated the mathematical treatment a little, but added to the accuracy of the data. Mid-ear width is a character by which both the Eastern and Mexican complexes differ from Basketmaker or Pima-Papago corn. Its score is accordingly divided by half and the halves are added to both the x and y axis. Husk striations on the kernel and compression of ear at the base are characteristic of Basketmaker and Pima-Papago corn and of neither the Eastern nor the Mexican complex. Their scores are accordingly added, the sum is halved and the result subtracted from both the x axis and the y axis.

All of this sounds rather complicated. In practice the calculations are really very simple. Let us take an actual instance. The ear known in our collections as CA. #240 was collected at the San Ildefonso pueblo. It is intermediately tapered, has 14 rows of kernels, and is undented. These three characters therefore contribute 1, 1, and 0, respectively to the index of the Mexican complex. The base of the ear is not perceptibly enlarged, the kernels are regular in shape and arrangement, they are 10 cm. wide, and the diameter of the shank just below the ear is 3.1 cm. By the score values as tabulated above, these four characters therefore contribute 0, 2, 1, and 2 to the Eastern Index. Adding the above individual scores gives sub-totals of 2 for the Mexican Index and 5 for the Eastern. The mid-ear width is 4.3 cm. which is in the intermediate range and therefore scores 1, giving us  $\frac{1}{2}$  to be added to each axis. The ear is not compressed at the base and has slight husk striations on the kernels. Its score for these two characters is therefore 1 plus 0. Dividing this by 2 gives  $\frac{1}{2}$ , which when subtracted from both totals cancels the previous  $\frac{1}{2}$  and gives us total scores of Mexican 2, Eastern 5. This ear therefore appears as a dot in fig. 15, two units up from the 0 point and 5 to the right.

The scale for the Mexican complex runs from a minus 2 to a plus 7 and the scale for the Eastern from a minus 2 to a plus 8. Theoretically, an idealized Eastern ear should score: y, 0; x, 9. Several ears of Sacred Flour Corn from the







Figs. 3-18. Scatter diagrams showing individual ears of maize measured according to a "Mexican Index" on the vertical scale and an "Eastern Index" on the horizontal scale. Further explanation in text.

Six Nations of New York state all were found to score: y, 0; x, 8. One ear of a primitive pointed dent maize from Michoacán, Mexico, scored: y, 7; x, 0. Much of the corn from the neighborhood of Mexico City scores: y, 6; x, 2. The material in our collections from the Pima, the Papago, and prehistoric Basketmaker maize scores either -2, -2 or somewhere between there and 0, 0.

The two indices plotted at right angles to each other give us, therefore, a comparison grid 9 units high and 11 units long. Its upper left-hand corner represents a sharply tapering, highly dented Mexican corn and its lower right-hand corner the big "crescent-seeded" types of eastern North America. The upper right-hand corner should denote corn in which both the Mexican and Eastern complexes are highly developed. It would therefore be a large-eared, large-shanked, wide-leaved corn, highly dented with many rows, and a markedly tapering ear which bulges at the base. Such a type of corn is fairly common in the more highly developed maize-growing regions in Mexico. In the Southwest it spread to such old Spanish-American communities as those at Santa Fe and Chimayo.

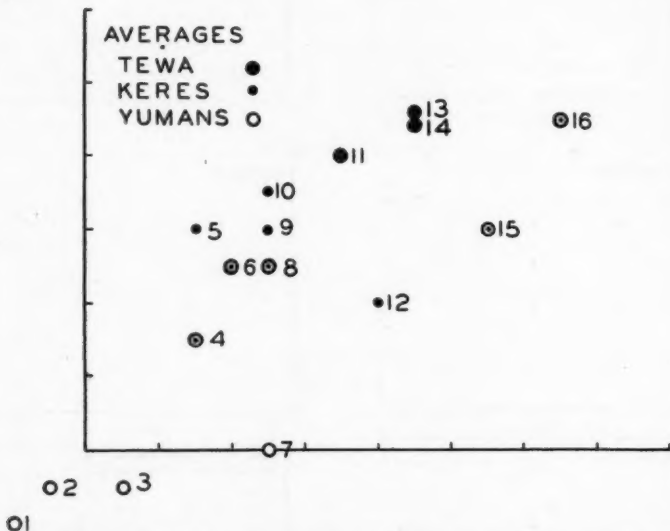


Fig. 19. Data of figs. 3-18 averaged by tribes. Language groups represented in part. Each symbol represents the average of all the measured collections from one tribe as in figs. 1 and 2. Dot-in-circle symbol is for various tribes not falling in one of the three designated language groups. 1 signifies Papago; 2, Yuma; 3, Mohave; 4, Hopi; 5, Cochiti; 6, Zúñi; 7, Havasupai; 8, Navaho; 9, Laguna; 10, San Felipe; 11, Isleta; 12, Acoma; 13, San Juan; 14, San Ildefonso; 15, Tesuque; 16, Chimayo.

We can use the grid in two ways, either to show the morphology of single ears with relation to these four extreme types or to compare the theoretical averages of particular collections. Our data from the Southwest are presented, tribe by tribe, in figs. 3-18. In fig. 19 the averages of each tribe are given for

comparison with each other. In fig. 20 the measured ears in our original collection are diagrammed, using the same grid as was used in figs. 3-18. When the entire lot is inspected in fig. 20, it is apparent that the maize of the desert-dwelling Indians is fairly well set off from that of the Pueblos. The Puebloan maize can be more or less arbitrarily divided into an intermediate type, and into Puebloan, which varies from strongly Eastern to strongly Mexican. In Table II the entire collection is presented in a tabular summary according to this classification.

When the above classification had been completed, instead of drawing dots on paper, a large table top was marked off with the appropriate squares and the actual ears were laid out on the enlarged grid. After this was done it was evident that the classification was quite a natural one (Anderson and Cutler, '42), since it put similar qualities together in addition to those which had been used in making the indices. This was particularly noticeable for color; the whites were strongest around the 0, 0 point and the red pericarp colors (P) were concentrated in the upper right-hand corner of the figure.

In short, an analysis of the color differences brings out the same points as the analysis of the shape and size differences presented above. Color is such a technically complex problem genetically that its analysis has been undertaken jointly with Dr. E. G. Anderson and the results will be published separately. The chief points brought out by this analysis are as follows: In so far as their color genes are concerned, the maize varieties of the Southwest are of two extreme types with numerous intermediates. One of these extreme types prevails among the Papago

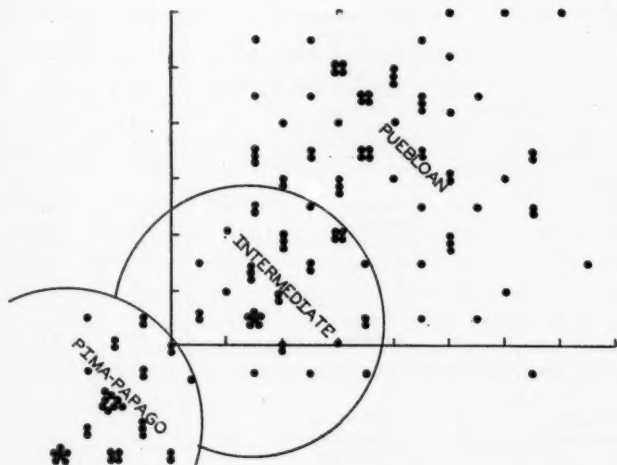


Fig. 20. Scatter diagram showing all the measured ears from the Southwest, using the same two indices as in figs. 3-19. Each dot represents a single ear.

and related tribes. It is a gene combination (ccrr) apparently common in west Mexico and in South America. It differs only slightly (though significantly) from that of Basketmaker maize. The other extreme type is characteristic of the eastern Pueblos while the maize of the western Pueblos consists of various combinations of these two extremes.

TABLE II  
MEDIAN VALUES

	<i>Number of ears measured</i>	<i>Prevailing sub-race or races of maize</i>	<i>Kernel diameter in mm.</i>	<i>Number of rows</i>	<i>Mid-cob diam. in mm.</i>	<i>Shank diam. in mm.</i>
<i>Desert Indians</i>						
Papago	62	Pima-Papago	9	12	36	14
Yuma	7	Pima-Papago	8	10	32	10
Mohave	5	Pima-Papago	10	10	37	11
<i>Hopi &amp; Neighbors</i>						
Havasupai	10	Pima-Papago & Intermediate	11	12	41	19
Hopi	19	Intermediate & Puebloan	9	14	38	18
Zuñi	7	Intermediate & Puebloan	9	16	40	23
<i>Keres-speaking Pueblos</i>						
San Felipe	7	Intermediate & Puebloan	9	16	41	24
Acoma	13	Intermediate & Puebloan	10	12	42	24
Laguna	16	Intermediate & Puebloan	9	14	43	22
Cochiti	5	Intermediate & Puebloan	9	16	44	24
<i>Tewan Pueblos</i>						
San Juan	5	Puebloan	9	16	45	34
Taos	6	Puebloan	9	12	42	32
Tesuque	6	Puebloan	11	12	43	34
San Ildefonso	14	Puebloan	10	14	44	32
Isleta	10	Puebloan	10	16	45	26
Nambe	3	Intermediate & Puebloan	10	14	38	30
Jemez	3	Puebloan	9	16	46	28
<i>Intrusives</i>						
Mescalero Apache	6	Intermediate	8	14	38	16
White River Apache	10	Intermediate & Puebloan	10	12	42	18
Navajo	26	Intermediate & Puebloan	10	14	41	22
Chimayo Sp. Amer.	4	Spanish	12	14	51	22
Santa Fe Sp. Amer.	3	Spanish	12	14	52	24

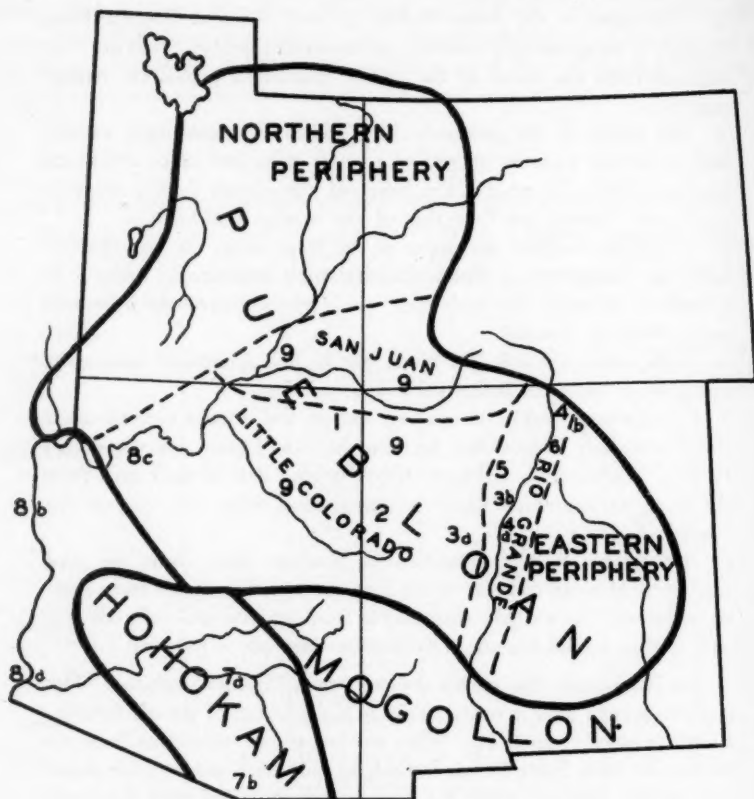
A number of facts are apparent from figs. 3 to 20:

1. The maize of the desert Indians (Yuma, Mohave, Cocopa, Pima, Papago) is comparatively uniform and essentially similar. It is not very different from the maize of the widely distributed prehistoric Basket-makers.
2. The maize of the pueblo-dwelling Indians is much more variable both as to the varieties grown by a single tribe and as to differences between tribes. In general, the maize of the eastern Pueblo people is much more Eastern-like than that of the western Pueblos.
3. Of all the Pueblos, the maize of the Hopi shows the least Eastern influence. Some of it is almost identical with Basketmaker maize. As a whole, it is rather like such corn which has been strongly influenced by the Mexican complex.
4. Zuñi maize is much like Hopi, but in our admittedly incomplete collections it lacks the Basketmaker-like varieties.
5. The Keresan Pueblos are all very similar and grow a type of maize which is roughly intermediate between the Pima-Papago and the eastern Pueblos. They might well have derived a good deal of their corn from the Hopi, an impression which is strengthened when the color is also considered.
6. The eastern Pueblos, considered as a whole, have about the same amount of Mexican complex as the Keresan, but show much more Eastern influence. As a whole, they are far from uniform and each one presents certain special features. By pueblos these are as follows:

*San Ildefonso*.—This pueblo shows a strong "Spanish" influence. This is not surprising since it is practically in the outskirts of the old Spanish-American town of Santa Fe. When the ears of our collections from the pueblo and from Santa Fe are laid side by side there can be little doubt that the San Ildefonso maize has been extensively mixed with that from the Spanish community near by.

*Isleta*.—With the exception of a few ears of maize, our collections from this pueblo are very similar to those from the western Pueblo area. This is to be expected since it is known that this pueblo took in a considerable number of Keresan-speaking refugees. Mrs. Parsons reports that clan structure shows resemblances to both Keresan and Tewa. Considering its location and its history it is therefore to be expected that the Isleta maize should include both types.

*San Juan*.—This maize is all very much alike and all similar to that from Mexican villages. This, too, is what might have been expected. The site of the first Spanish settlement in the Southwest, San Gabriel de los Españoles, is just across the river. The mission was succeeded by a little Mexican town, "Chamita", which was unfortunately on the right-of-



## KEY TO MAP OF THE SOUTHWEST

## ARCHAEOLOGIC AREAS

## Puebloan area:

San Juan—the early center of development.

Little Colorado—area of early expansion.

Northern Periphery—an area briefly occupied after 1000.

Rio Grande—area of late settlement; present sites of most pueblos on river bottoms with irrigated fields a post-Spanish innovation.

Eastern Periphery—late eastward expansion, abandoned in post-contact times.

Hohokam area: A major culture province of differing origin from the Puebloan.

Mogollon area: A major culture province of controversial origin; suspected of being Eastern in its derivation.



## KEY TO TRIBAL AND LINGUISTIC GROUPINGS

<i>Language group</i>	<i>Pueblos or tribes</i>
1. Shoshonean	Hopi (First Mesa: Sichomovi, Walpi, also the Tewa village of Hano since about 1700; Second Mesa: Mishongnovi, Shumopovi; Third Mesa: Oraibi, Hotevilla, Bacabi)
2. Zuñian	Zuñi
3. Keresan	{ a. Laguna, Acoma b. Cochito, Santo Domingo, San Felipe, Zia, Santa Ana
4. Tiwa	{ a. Isleta, Sandia b. Taos, Picuris
5. Jemez	Jemez, Pecos, (Pecos joined Jemez, 1838)
6. Tewa	Nambe, Tesuque, San Ildefonso, San Juan, Santa Clara
7. Piman	Pima, Papago
8. Yuman	{ a. Yuma b. Mohave c. Havasupai
9. Athapaskan	Navaho, Apache

*Notes.*—Shoshonean was widely spread in the Great Basin, but only the Hopi took on Puebloan culture. Zuñian is of unknown relationship. The Tiwa, Jemez, Tewa, Keresan all belong in the Tanoan speech family, which is suspected to be of Eastern origin. The Piman are a northwest Mexican group. The Yuman seems to be an old group in the area. The Athapaskans are the latest entries into the area, probably beginning to drift in after 1000 A.D., and settling in between the Pueblos.

way of the railroad when it came through. The Mexicans accordingly moved across the river to join the pueblo of San Juan, which must have been in a depleted condition to have accepted recruits from outside the pueblo.

*Taos*.—While a larger collection from this interesting pueblo would be highly desirable, even our small collection seems to be significant. It includes some typical Pueblo types and two ears which are almost purely Eastern. This accords with the general Eastern cultural affinities of the Taos pueblo.

*Tesuque*.—While none of the ears from the pueblo are as purely Eastern as some of those from Taos, the general average is more Eastern than is that of any other pueblo. Tesuque is generally thought to be a Pueblo "shell" which was taken over by a non-Puebloan people. Judging from the maize alone, these newcomers might have been related to (or in close contact with) tribes of the Great Plains.

The significance of these conclusions must be placed against a background of southwestern culture history. There are in the Southwest two well-known basic cultures, the Anasazi and the Hohokam. There may well be a third, the Mogollon culture. The first two are the best known and our agricultural material relates to them. The Mogollon culture will, therefore, be reluctantly omitted from this discussion.

The two basic cultures with which we are concerned are the Anasazi and the Hohokam (see Map). Anasazi is a term used to refer to the culture which developed in the plateau region of the Southwest. The evidence to date shows that the Basketmakers, a non-agricultural people who had been living by hunting and gathering, learned of agriculture and began about 300 A.D. (or possibly earlier) to grow corn and squash (*Cucurbita moschata*). These agricultural beginnings are usually placed in the "Four Corners" region (adjacent corners of Arizona, Utah, Colorado, and New Mexico). The crops and the idea of farming are clearly derived from some outside source.

Farming was apparently of minor importance in this early period. Crops may well have been handled as they were by some of the early historic Apache; i.e., corn and squash were planted and left to survive as best they could while the tribe went off hunting and gathering.

At a later period (500–700 A.D., Basketmaker 3) the Basketmakers show evidence of further contacts with some outside culture, and further cultural changes occurred. Pit houses were built (no houses are known from the earlier periods), pottery making began, and more varieties of corn appeared.

Around 700 A.D. more cultural changes occurred and sufficient new traits were introduced that a new cultural designation, Puebloan, is given. The first Pueblo period (700–900 A.D.) centered in the old Basketmaker area. Cultural developments, e.g., house types and pottery types, continued and further intro-

ductions of corn types are probable.

In each of these preceding periods there was some expansion outward from the central area in the "Four Corners" region. This expansion reached its maximum between 900-1100, Pueblo 2. People related to the Pueblo (Anasazi) culture then extended from southeast of Flagstaff, Arizona, nearly to Salt Lake, and in the latitude of the Grand Canyon reached from the Rio Grande to the Colorado. There was considerable regional variation. Large, many-roomed pueblos were already being built in the Chaco Canyon, the people of Mesa Verde were living in small masonry houses, while pit houses remained in use near Flagstaff. In all areas, however, the people were fully sedentary agriculturalists.

From the very beginning these people had been occupying a distinctly arid country and raising crops by dry farming. They must, therefore, have started with highly specialized crops. By locating their fields advantageously in reference to soil, run-off, and higher elevations with their greater precipitation they succeeded for hundreds of years in raising crops in areas considered impossible for modern agriculture.

In Pueblo 3 (1100-1300) a shrinking of the occupied area became apparent, and the settlements of small villages of loosely grouped houses now became compact towns of considerable size which were often built in defense locations. Houses were built wall to wall, several stories high, and entrance to first-floor rooms was normally from the roofs and not from the exterior ground level.

The attempted explanations for these happenings are still unreconciled. They fall into three categories. One theory points to climatic changes; another points primarily to the effects of invasion of nomadic peoples; a third to soil exhaustion and erosion. A variant of the second calls attention to the effect of warfare between the various Pueblo peoples.

That the distribution of corn types fits both the linguistic grouping and geographic position has already been pointed out. This may either imply that the various linguistic groups brought varying races of corn or that their geographic position in the Southwest gave them greater or lesser opportunities to get new varieties of corn. In view of the conservatism of the people, the high degree of adaptation of some of the earliest corn types, and the sudden appearance of new races of corn in special areas (e.g., dent corn of extreme Mexican type in the Northern Periphery), it seems fairly possible that the various linguistic groups represent different immigrations of people, each of which brought new agricultural material. The time of these introductions is not yet established, but further research now under way may do much to clarify this.

Perhaps a movement of peoples is implied in the first appearance of corn in the Four Corners region. Clearly, there were further introductions of corn types, between Basketmaker and Pueblo times. Whether other introductions occurred in the 600 years between Pueblo 1 and the "great drought" of 1300, or whether the next importation of corn came with peoples unsettled at the time of the "great drought" is not yet clear. It is even quite

possible that some of the corn types limited to the upper Rio Grande pueblos are post-Spanish, for after the Pueblo revolt some of the people are known to have fled into the Plains. It is not unlikely that some of these people later returned to the Rio Grande bringing new maize varieties with them, e.g., to Tesuque.

It is clear from the above that the development in the Anasazi area was a very complex affair involving different peoples and cultures. The cultural evidence suggests that in the thousand years after the introduction of agriculture there were repeated movements of people into the area. The implication of multiple introductions is particularly strong in the languages represented.

We are quite clear on the fact of multiple introductions of corn into the Pueblo area. We are sure of separate corn varieties appearing in Basketmaker 2 and again in the Basketmaker 3-Pueblo 1 periods; thereafter we can not yet place the time of arrival of the various races of corn that are modernly represented in the Anasazi area. Further work will surely make this possible.

The other basic culture of the Southwest to be considered here is the Hohokam. It is both less well known and less complex. Our knowledge concerning it begins about 600 A.D. according to Gladwin ('42, p. 4). At this time it seems already to have been a developed culture with agriculture and pottery, hence its true beginnings must go back of that date. The people lived in loose villages and occupied the middle Gila and the Salt River valleys, areas utilizable in their lower parts only by irrigation, whether from arroyo flooding or by using the waters of major streams. True canal irrigation was developed very early. Although we know less of this culture than we do of the Anasazi sequence, the evidence to date shows no such complexity in development as is found on the plateau. Culture periods are discernible but in the main they seem the result of local development with little outside influence until very late in their history.

The great problem of the Hohokam centers on their survival. After the mid-14th century the record becomes very incomplete. When the Spanish arrived they found the Hohokam area occupied by the Pima-Papago peoples. These latter were, and remain, village-dwelling farmers retaining the old Hohokam crops and some irrigation. The agricultural evidence suggests that they may be (at least in part) the descendants of the Hohokam.

A great contrast runs throughout these two cultures. The Anasazi developed into town-dwelling peoples with a tradition of masonry houses; they specialized in dry farming, developed elaborate rituals for rain, and had distinctive pottery techniques, etc. Their culture was complex, perhaps partially because of the different elements entering into its make-up. The Hohokam remained village dwellers with little evidence of alien peoples or cultures influencing them. They very early developed irrigation and established an elaborate ditch system in the Gila and Salt valleys. In religion, art forms, specific crops, and many more details they differed markedly from the Pueblo peoples.

This contrast is clearly reflected in the corn of the Southwest. Pueblo corn is complex in its make-up. It changes from period to period and to-day varies

throughout the Pueblo area. By comparison with the maize of other native areas, Hohokam maize is extremely uniform, probably one of the most uniform races one will ever find under primitive cultivation. It seems to have changed little in the past thousand years.

One of the crucial points in the relation of the Anasazi and the Hohokam revolves around the relationship between Basketmaker corn and Hohokam corn. We know Basketmaker corn from its preservation in the dry caves of the Southwest. It is closer to the Hopi and the Pima-Papago corn of to-day than it is to the maize of the Rio Grande pueblos. Some of the strains of Hopi corn fairly represent late Basketmaker corn. Hohokam corn is known from the published reports of the Snake Town plant materials (Castetter and Bell, '42), and from Haury's excavations in Ventana Cave (paper in press, 1944, but we have examined the maize remains). It is close to, though not identical with, the corn grown to-day by the Pima and Papago Indians. We have therefore a distinct race of corn in the Southwest that is common to the two different cultural areas at the earliest levels and which survives in part among the westernmost of the Puebloan peoples and among the desert-dwelling peoples who are presumably the descendants of the Hohokam.

We have not yet photographed and measured all the prehistoric North American corn available in museums and private collections. Until that job has been done an extended discussion is premature. However, from the prehistoric maize we have already seen and the junior author's studies of modern Mexican maize, it seems probable that there were at least three waves of prehistoric maize in North America. The first was a small-cobbed, small-seeded, tessellated, compressed, undented race. It survives to-day in its purest form in the maize of the Pima and Papago. It can be seen only slightly mixed in the early varieties of the Pawnee and other Missouri River Indians, in old varieties from the Gaspé Peninsula in Canada, and in *Maíz reventador* and related varieties from western Mexico. Its presence in Oaxaca, Mexico, in 400 to 600 A.D., is suggested by the representations of maize on the funerary urns of the Zapotecs, which resemble Basketmaker maize more closely than they do the modern varieties of Oaxaca. It is one of the types recovered from mounds and other archaeological sites in the Mississippi Valley (where it is apparently one of the earlier types to appear, though the evidence is not consistent on this point). The other two waves we have already described as "Mexican" and "Eastern." In later papers we hope to be able to work out the order of their appearance and perhaps ultimately to trace them back to their origins.

#### SUMMARY

1. The technical advantages of *Zea Mays* for cytological, genetical, and archaeological study are described. It is concluded that when we eventually combine the information from these three disciplines we shall have a more complete picture of maize in space and in time than will ever be possible for any other



world crop.

2. Because of its geographic and climatic isolation, southwestern maize is simple in its variation pattern as compared with that of Mexico or Guatemala.

3. The importance of collecting samples from remote and relatively conservative Indian communities is discussed.

4. One of the most significant maize characters in the Southwest is the denting of the kernel due to a cap of soft starch. Its genetics is obscure but a large number of genes are involved. Much of the denting of Indian varieties in this area is of such slight grade that it might readily be overlooked. Breeding experiments have proved that even the slight grades of it in that area are genetically controlled and are not merely due to harvesting when immature.

5. Maize in the Southwest has come from at least four different sources: the Basketmakers, the Hohokam, the Mexican plateau, and eastern North America. The maize of the Basketmakers and of the Hohokam was very similar but apparently distinct.

6. In the Southwest the following three characters of the maize ear are correlated: ear taper, row number, and denting of the kernel. They are referred to as the Mexican complex of characters. Kernel width, shank diameter, an enlarged butt to the ear, and straight rows are also correlated. They are called the "Eastern" complex.

These eight characters and two others were used in constructing two indices for measuring southwestern corn. Plotted on x and y axes they form a "comparison grid" on which scatter diagrams of the maize from one pueblo may be compared with the maize from another, or on which the average values of different collections may be similarly compared.

7. Scatter diagrams are presented for a portion of our collections of modern maize and a summary of the conclusions drawn from them is given on pages 309-312.

8. An attempt is made to interpret these findings in terms of what is known about the history of the Southwest from the beginnings of agriculture to the present. The following hypotheses seem fairly well established:

A. The Basketmakers and Hohokam brought similar, though non-identical, strains of maize into the area. The Hohokam maize apparently was brought up the west coast of Mexico and has remained with only slight modifications as that now grown by the Pima and Papago.

B. The maize of the early Basketmakers was progressively modified more and more in the direction of the maize of the Mexican plateau, causing an increase in row number and in the amount of denting of the kernel.

C. The maize of the Southwest was greatly modified from 1200 to 1300 A.D. The complex of characters introduced at that time is characteristic of the eastern United States and the easternmost pueblos were most affected and the westernmost the least.



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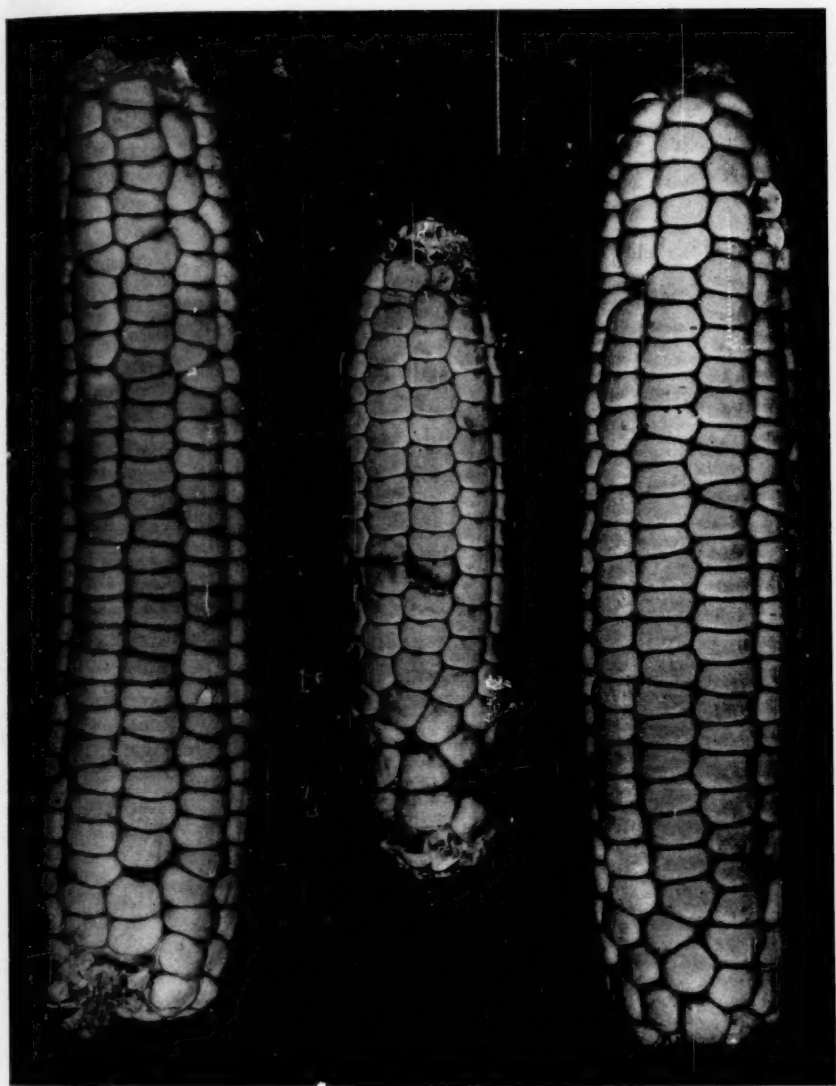
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## EXPLANATION OF PLATES

Plates 2-4 are from the special collection of maize photographs assembled in the Museum of Anthropology of the University of California at Berkeley. We are indebted to E. W. Gifford for permission to reproduce them. All three illustrations were photographed, printed, and reproduced at approximately natural size.

## PLATE 2

Papago white flour corn. Three ears purchased from Mrs. Margaret Harvey (Xavier) at Choulick, near Sells, Arizona, on the Papago reservation, by Edgar Anderson and Emil Haury. In the Anderson collection they are Choulick Nos. 1-3, from left to right in serial order. Their scores on the two indices used in this paper are as follows (in each case the Eastern Index is given first, followed by the Mexican Index): —2, —1; —2, —2; —2, —2.

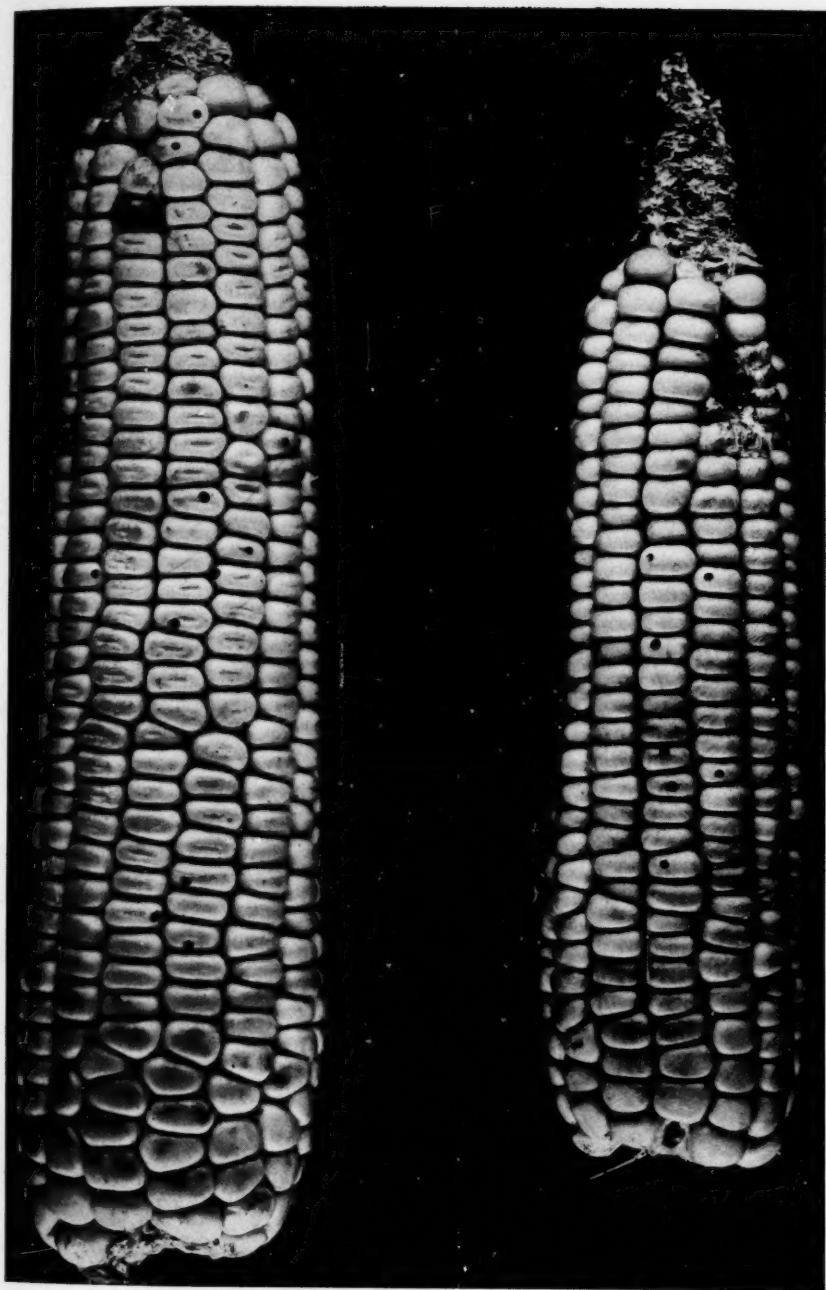


CARTER & ANDERSON—MAIZE IN THE SOUTHWEST

## EXPLANATION OF PLATE

## PLATE 3

Hopi white flour corn. Right, Carter No. 497, left, Carter No. 498. The former scores 1/2 on the Eastern Index and 1-2 on the Mexican Index. The latter scores 2, 3. Note the faint crease or "dent" at the apex of some of the kernels. This degree of denting is commonly found in Hopi flour corn.



CARTER & ANDERSON—MAIZE IN THE SOUTHWEST

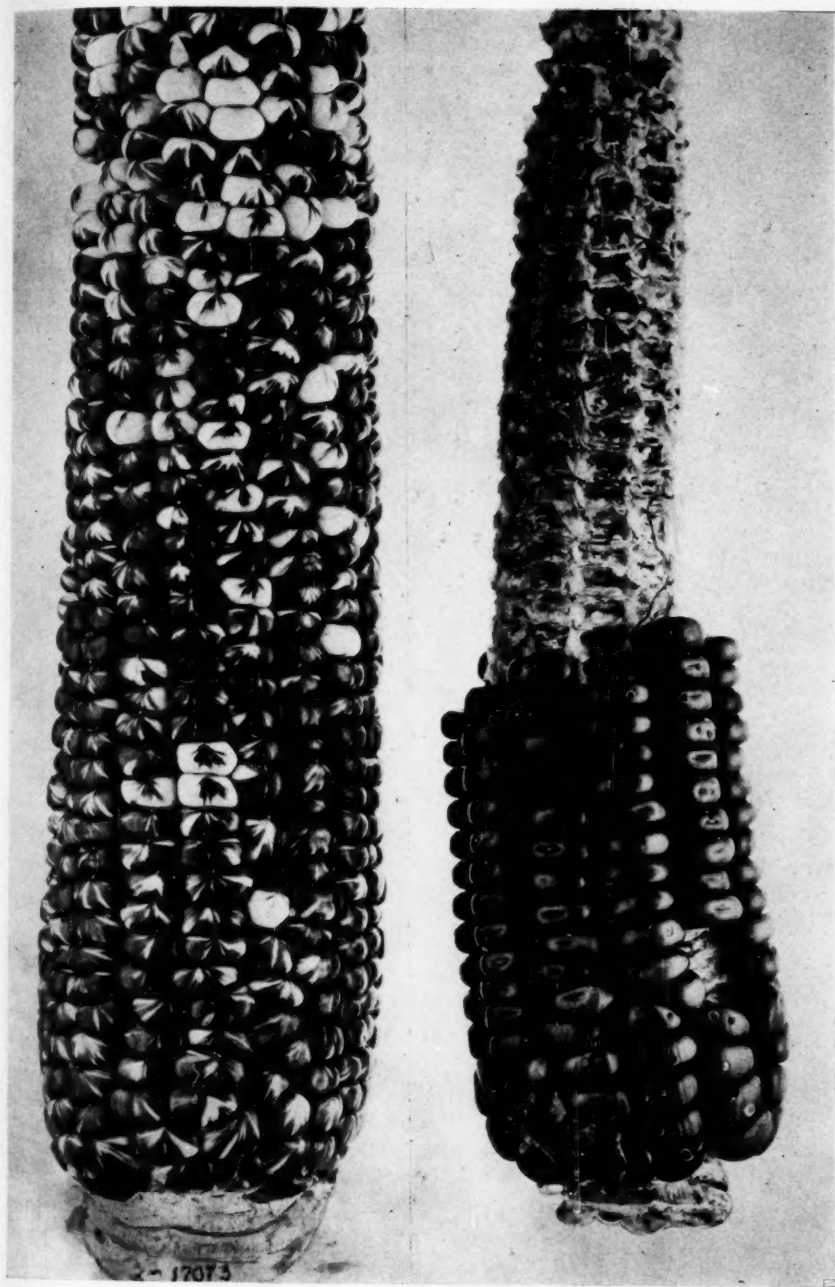
## EXPLANATION OF PLATE

## PLATE 4

Right, Isleta red corn. Carter No. 315, scoring  $6\frac{1}{2}$  on the Eastern Index and  $2\frac{1}{2}$  on the Mexican. Note the wide seeds and the straight rows of uniform kernels.

Left, Tesuque red-and-white corn (mosaic pericarp). Carter, scoring 4 on the Eastern Index and 5 on the Mexican. At the base of the photograph note the heavy, well-developed shanks which support the ears. These are characteristic of much modern Pueblo corn but did not appear in most of the Southwest until after 1200 A.D.





CARTER & ANDERSON—MAIZE IN THE SOUTHWEST

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## CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS

### VII. SOME PTERIDOSPERM STEMS FROM IOWA

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The occurrence of richly fossiliferous coal balls in the Upper Pennsylvanian rocks of Iowa has been reported by Darrah in 1939 and 1941. In the latter paper he gives a list of the species observed as well as a brief discussion of the dominant floral elements. The distribution and occasional abundance of these petrifications in Iowa is now sufficiently well known so as to render a detailed review unnecessary, but certain introductory remarks are in order relative to the general floristics, as compared with the Illinois coal balls.

In September, 1944, Mr. Frederick O. Thompson of Des Moines very generously turned over to the writer, for study and preservation in the Henry Shaw School of Botany, a selected portion of his remaining coal-ball specimens. All of this material was collected from the highly prolific, although now abandoned, Urbandale mine located on the north side of U. S. Highway No. 6, 1.2 miles west of the city limits (63rd Street) of Des Moines. The coal seam from which the petrifications were obtained lies 185 feet below the surface, the elevation of the latter being 805 feet. It is regretted that a more precise stratigraphical position, other than "the Des Moines Series," cannot be given at this time. The author has been informed that a detailed study of the stratigraphy of this region will be published shortly, and it is hoped that this information may be given in the next number of our "Contributions" which will deal with seeds from the Urbandale coal balls.

Our collection consists of approximately 110 cut slabs which vary from 3 to 20 cm. in diameter. It is admittedly small as coal ball collections are accounted, yet rich in the number of seeds, leaves, pteridosperm stems, fertile fern-like foliage, and other plant parts, many of which are either striking novelties or very imperfectly known.

During the three years prior to the war the paleobotanical work in this laboratory was devoted very largely to a study of fossil plants from certain southern Illinois mines.<sup>1</sup> Although the progress made in that region constitutes but little more than a bare introduction to the field work lying ahead, it does seem clear that the Carboniferous flora that occupied much of southern Illinois was dominantly pteridophytic. Certainly the Herrin coal from the great Pyramid strip mine south of Pinckneyville was formed to a very considerable extent from the remains of *Lepidodendron* (Pannell, '42), and the roof shales above the same coal in the

<sup>1</sup> See parts I-VI of this "Contributions" series, in *Ann. Mo. Bot. Gard.* 29-30. 1942-43.  
Issued September 15, 1945.

Old Ben mine #11, in Franklin County, display a preponderance of arborescent lycopods, articulates, and ferns.

*Lepidodendron* is so preponderant in the Pyramid mine coal balls that we have on numerous occasions all but decided to abandon further collecting there, yet the constant lure of fragments of other plants has brought us back time and again, and it is very probable that this will continue for some time.<sup>2</sup>

It seems reasonably safe to express the opinion that the study of coal balls is a phase of paleobotany that promises to be long and productive. It is only in England that anything approaching exhaustive studies has been carried on, and even there we have no reason to assume that the task is completed. The works of Williamson and Scott, and a number of other British paleobotanists of Scott's period, were based on coal-ball petrifications, yet few of these investigators were collectors. If we may judge from Scott's written works and his magnificent slide collection, his source of supply was primarily through the medium of professional collectors and other persons. Thus only the more striking and obviously new things reached his hands. Perhaps it would be asking too much to expect one man to contribute more, yet I cannot help but feel that Scott's contributions would have had an even more vital effect on the following generation had he personally supervised the cutting of some few tons of coal balls in his own laboratory.

Judging from our own experience in Illinois and from Mr. Thompson's vast collections, most of which are deposited at Harvard University, it seems clear that large-scale collecting is the primary requisite to the restoration of reasonably complete plants and their assemblage into correspondingly complete paleo-landscapes. Studies of the flora of an individual coal ball are certainly a thing of the past. Productive mines must be revisited many times and collections considered in terms of tons. This may savor of mass production rather than "scientific procedure," yet it is the only way in which scattered parts of the plants may be brought together and those plants assembled into representative restorations.

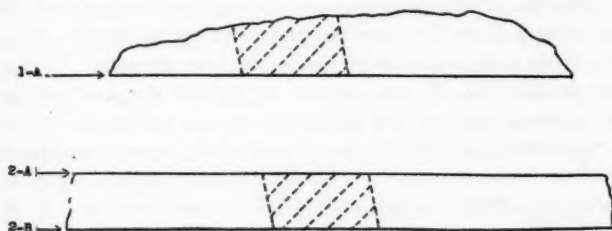
To return to the Pyramid coal balls, evidence of seed plants in the petrifications from that mine are meager indeed. Apparently they were not abundant in the immediate environs, and the Urbandale specimens from Des Moines thus present a most striking contrast. Although fern-like fructifications are present in some abundance the Lycopods are comparatively rare, their place being taken by an extensive array of seeds, Cordaites stems and leaves, and stem-remains seemingly referable to the Pteridospermeae. From this assemblage the latter have been selected for primary consideration.

#### *Medullosa Thompsonii* sp. nov.

The following description of this stem is based on two slices cut from a coal ball approximately 15 cm. in diameter, one being an end cut. Both are approximately 1.5 cm. thick, and the stem passes through both pieces. Between these two

<sup>2</sup> In a collection of coal balls obtained from the Pyramid mine in December, 1944, one contains numerous specimens of *Cordaianthus* which is, judging from a preliminary study, closely related to *C. Shuleri* Darrah. In view of the frequent occurrence of *Metoxylon* it is not surprising that *Cordaianthus* should have turned up, although this is the first record of it from that region so far as I am aware.

portions of the original coal ball, one or two slices, apparently totaling a little more than 3 cm. in thickness, have been removed. Mr. Thompson, the collector, has informed me that this intermediate portion was one of the specimens sent to the Botanical Museum at Harvard University some few years ago which have not been available for study. There is, however, no doubt as to the relationship between the two pieces in our collection.



Text-fig. 1. Sectional view through coal ball WCB420, with approximate position of *Medullosa Thompsonii* stem shown in shaded area; 1-A represents face A of block 1, and 2-A, 2-B represent faces A and B of block 2. Reduced about one-half.

Aside from its other significant features, this stem (and the remains of other Medullosan stems, petioles, roots and leaflets in associated coal balls) is of special interest in that it demonstrates stelar fusions more clearly than has been reported in any previously described species of the Anglorota (Schopf, '39) group. Text-fig. 1 shows the order in which the preparations were made.

#### *The Stem and Leaf Bases.*—

The stem measures approximately 4.3 x 3.0 cm., exclusive of the petiole base shown at the left in fig. 1. It is slightly crushed and must have been cylindrical, or nearly so, measuring about 3.6 cm. in diameter in life. It consists of three sharply defined regions: an outer fibrous cortex (rind) which certainly contributed appreciably to the support of the plant, a broad inner parenchymatous cortex, and a central stelar system bounded externally by a band of periderm. Every section also displays the bases of at least one or two petioles in various stages of departure. It is possible to distinguish sharply between petiole base and stem only where the rind is in the process of developing between the two. Thus in fig. 1 the partitioning fibrous tissue is shown developing at point *a*, preparatory to the departure of the petiole at the left.

Those who are familiar with the Medullosas will observe an unmistakable similarity between this stem and the English *M. anglica*. A number of differences will be pointed out in the course of the description which, it is believed, adequately justify the distinct specific designation.



The rind is bounded by an epidermis consisting of brick-shaped cells slightly elongated radially (fig. 32). The radial, and especially the outer walls, are somewhat thicker than the inner ones. This is probably accounted for, in part, by the former presence of a cuticle, although it has not been possible to distinguish this from the wall of the epidermal cells.

The cortical cells, which are small and nearly isodiametric immediately within the epidermis, gradually increase in size, attaining a maximum within the fibrous zone. In *Medullosa anglica* the outermost cortical layer is illustrated (Scott, '99, fig. 13) as being palisade-like after the fashion of the epidermis. No such differentiation of the outer cortex is present in the Iowa specimen. In cross-section the fibrous strands (fig. 5) are circular to slightly elongate radially. These anastomose, although only at very extended intervals, and appear in longitudinal section as very nearly parallel strands. An especially noteworthy feature of this part of the stem lies in the rarity of associated secretory canals. They are present deeper within the cortex although markedly less conspicuous than in *M. anglica* and other related species.

It may be noted that in fig. 1, from approximately points *b* to *c*, the fibrous strands are lacking. The rind is replaced in this region by a periderm (fig. 33) consisting of an outer uniform layer of phellem 4 to 5 cells deep; within this there is a somewhat broader band of phelloderm of less regularly aligned cells which merge with the larger cells of the cortex within; and in between these two tissues lies what apparently was the phellogen. These terms are used as they are conventionally applied to living plants on the assumption that they correspond to the respective tissues of a normal periderm. In his description of *M. anglica*, Scott mentions a similar "distinct interruption of the hypoderma cortical fibers between the bases of adjacent leaves," and he suggested that it was in this region that the adventitious roots were inserted. While it is not possible to confirm this with *M. Thompsonii* it seems very likely that such may have been the case. Although *Medullosan* roots are abundant in other associated coal balls none were found in organic connection with the stem. This might be explained by the fact that our specimen probably represents a fragment of the plant from some distance above the ground.

The internal or stelar periderm differs in no way from that of other related species. At the level of the stem represented by surface A of block 2 it encloses three steles, lettered *x*, *y*, and *z* in fig. 2. The ground tissue immediately surrounding the steles is not sufficiently well preserved to merit further consideration. The steles vary with respect to size and development of secondary xylem. Stele *x* measures approximately 7.0 x 3.5 mm. and is somewhat crushed; stele *y* is 2.0 mm.; and stele *z* is 6.0 x 3.0 mm. in diameter.

Like the periderm, the primary wood seems to present no characters of special distinction. The secondary wood, however, is notably endocentric, being (Schopf, '39, p. 203) weakly developed towards the outside (fig. 2). Although the relative arrangement of the three steles has been slightly distorted, the position they



occupy in block 1, where all three are fused together (fig. 3), is the same, indicating that their position as illustrated in figs. 1 and 2 is but little changed from that in life.

By far the most interesting feature of this *Medullosa* stem lies in the fusion of the steles between the A surfaces of blocks 1 and 2. It may be noted in fig. 3 that stele *y* has clearly united with *x* while the union of *z* with the *x-y* fusion is in its initial stages.

The leaf traces depart from the steles as comparatively large (slightly less than 1 mm.), nearly cylindrical masses of xylem (fig. 14a). The initial trace almost immediately starts to divide (fig. 14b), forming the numerous collateral bundles (fig. 5) scattered through the massive parenchymatous cortex between the periderm and rind. Where the bundles are still in close proximity to the steles they are usually enclosed by a distinct sheath, although this is not as strongly developed farther out in the cortex.

An especially distinctive feature of *M. Thompsonii* is the comparative paucity of fibrous tissue in association with either the bundles or the secretory canals. Conspicuous sclerenchymatous sheaths or strands such as are figured for *M. distelica* (Schopf, '39, fig. 5) and *M. Noei* (Steidtmann, '44, pl. VI, fig. 1; pl. VIII, fig. 1) are not found in *M. Thompsonii*.

#### *Discussion of Stelar Anatomy and Comparison with Other Species.—*

Stelar fusions and stelar branching were evidently frequent in the stems of the highly complex Permian species (Seward, '17, p. 104). That the same events take place in the structurally simpler species of the Anglorota group is known only in a very sketchy way. In her description of *M. centroflis*, De Fraine noted the fusion of two steles, but at the point of fusion the steles are fragmentary (De Fraine, '14, pl. XV, fig. 2), and it was not possible to illustrate clearly the phenomenon. Scott referred to an interstelar fusion in *M. anglica* but here again the preservation was imperfect.

It is important that we have a clearer knowledge of this phase of *Medullosan* anatomy, partly in order to evaluate correctly the taxonomic use of stelar number and size, and partly to aid in interpreting phylogenetic trends in the group.

Professor Bower's investigations in the ontogeny of the ferns, the mature stelar systems of which are often rather complicated, indicate that the steles invariably started as a single protostele. It is hardly conceivable that the stelar ontogeny of the *Medullosas* could have followed any other course.

Numerous writers have compared the individual steles of *Medullosa* with the single stele of *Heterangium*. That portion of the stelar system shown in fig. 3 presents a rather close approximation to the *Heterangium* type. Whether or not the fusion of stele *z* with the already fused *x* and *y* steles became complete, resulting in a more nearly cylindrical (single) form, cannot be determined since the stem passes out of the coal ball shortly beyond the point illustrated. Even though the stele should assume a perfectly cylindrical form at a higher level there is, of

course, no implication that it should be referred to *Heterangium*.<sup>3</sup> There is no doubt, however, that such a stem fragment, if found isolated, would present a striking resemblance to that genus, at least as far as the stele is concerned. Inasmuch as the seedling of *M. Thompsonii* almost certainly started with a single stele it seems likely that divisions and fusions occurred rather regularly through the length of the stem.

A number of reviews dealing with Medullosan relationships have appeared during the past few decades, and there is no cause for adding to this literature at present except for the Anglorota subgenus. This subgenus was created by Schopf in 1939 with *M. anglica* as the type species. Other species that may be included are *M. centrofilis* De Fraine, *M. pusilla* Scott, *M. distelica* Schopf, *M. anglica* var. *thiesseni* Schopf, *M. Thompsonii* Andrews, and the *Medullosa* illustrated in fig. 7 (see p. 335). There can be no doubt that these constitute a very closely related assemblage, distinct in certain seemingly valid characters, yet similar enough to justify speculation concerning their interrelationships.

Before attempting any such racial considerations it is very necessary to determine in so far as possible what characters may be of taxonomic value and what ones are too variable within an individual specimen. In order to facilitate comparison of the above seven species they are shown, all at the same magnification, on plate 12. It is evident that their structure is pronouncedly similar in spite of the considerable size difference between the large *M. anglica* and the comparatively minute *M. pusilla*. The group is a remarkable one from the viewpoint of structure and certainly a closely related taxonomic unit, and there is no longer any doubt that it was widely distributed during the Pennsylvanian. Whether the species names that have been used to designate these stems would stand if the entire plants were known is, of course, not now possible to determine. In any case, the answer would not detract from their interest, and temporarily at least they have been handled in the most expedient way.

It seems unlikely that quantitative differences, such as size of the individual steles and the number composing a stem, can be allowed to bear much taxonomic weight. In *M. anglica* alone the steles are reported to range from 6 to 30 mm. in diameter and the almost continuous range throughout the group is clearly shown in figs. 23-30. Knowing the wide variation that may exist in both primary and secondary stelar bodies of fossil and living plants (Bower, '30; Pannell, '42), such characters must obviously be regarded with considerable deliberation. Neither is the number of steles in itself an entirely dependable character. Three is apparently the "typical" number in *M. anglica*, *M. Thompsonii*, *M. anglica* var. *thiesseni*, and *M. pusilla*, and it is more than likely that fusion took place in the stem of *M. centrofilis* resulting at certain levels in three steles.

<sup>3</sup> It should perhaps be shown that we are dealing with a fusion here and not a division; i. e., that the sequence is being read in the proper direction. Although the stem fragment is short it is clear that the petiole shown in fig. 1 (from which fig. 2 is magnified) is in a more advanced state of departure some 1.5 cm. farther along the stem (from the point at which fig. 3 is taken). This is indicated by the more nearly complete development of the rind separating the petiole from the stem.

De Fraine in her discussion of the affinities of *M. centrofilis*, notes that "the agreement in practically every detail between the steles of the specimen and those of *M. anglica* and *M. pusilla*, leave no doubt as to its very close relationship with those fossils." The relative extent of endocentricity in the steles of different species may present a character of value; at least *M. distelica* seems to display this to a more marked degree than the other species. Whether or not this varies appreciably through the course of an individual stem remains to be determined when longer specimens are discovered.

Aside from these variable characters of the stelar system itself, considerable weight has been attached to the presence or absence of secondary tissues accompanying the leaf trace on its departure from the stele. This secondary wood is conspicuously abundant in *M. anglica* but was reported absent in *M. pusilla* and *M. centrofilis*, and absent or very weakly developed in *M. distelica*. It is likewise absent in *M. Thompsonii*. As far as the leaf traces themselves are concerned they appear to present a very marked uniformity in all of the species described above. The nature of the accompanying fibrous sheath may, however, be of taxonomic value.

*Medullosa Thompsonii* differs from *M. anglica* in the comparative rarity of secretory sacs in the cortical rind, as well as the parenchymatous middle cortex. The hypodermal cells in the two are likewise divergent in their structure (c. f. Scott, '99, fig. 13; and fig. 32 of this paper). Although the Iowa stem and *M. anglica* are undoubtedly closely related the differences that have been noted seem to justify segregation.

The differences in number, size, and extreme endocentricity of the steles, as well as abundant development of secretory sacs in the cortex, clearly set *M. distelica* apart from the Iowa specimen. Of the figures in plate 12, this leaves only *M. centrofilis* and *M. pusilla*. If size has any significance in classification the latter certainly deserves its own pigeon-hole, and the secretory canals are reported by Scott as numerous.

Although they are interesting and illustrate the size range in the Anglorota group I do not feel that either *M. anglica* var. *thiesseni* or *M. sp.* (fig. 7) is sufficiently well preserved to allow of precise comparison. *M. anglica* var. *thiesseni* and *M. Thompsonii* may very possibly be one and the same species but this cannot be verified until supplementary material of the former is forthcoming, showing well-preserved extra-stelar tissues.

Thus of the previously described species of *Medullosa* which present sufficiently well-preserved detail to allow of precise comparison, *M. centrofilis* appears to be the most closely related to the Iowa fossil. The differences are not great, the central "star-ring" and the secretory canals in the cortex of *M. centrofilis* being the only conspicuous points of divergence.

#### *Leaves.*—

Numerous isolated petioles or rachis fragments belonging to *Medullosan* stems

are present in the Urbandale coal balls. They are not only abundant but represent, as well, different branching orders of the leaves, as is clearly evinced from the size variation and the anatomy of the rind.

From a study of the literature and the material at hand, it appears that the following characters are most significant in the classification of these fossils: structure of the fibrous strands composing the rind; presence or absence of the secretory ducts, their distribution, and whether or not they are regularly associated with the fibrous strands; distribution of the vascular bundles. Use of the last character is restricted to those specimens in which there is no appreciable amount of crushing or distortion.

A number of the better-preserved specimens agree closely enough with the attached petiole bases of *M. Thompsonii* to warrant their inclusion under that species. These isolated petiole and rachis remains<sup>4</sup> (figs. 9, 12, 13, 19) vary from 16 mm. (fig. 9) to a little over 4 mm. (fig. 12) in diameter. The diameter of the leaf base shown about to depart from the stem in fig. 1 measures approximately 2.2 cm. in diameter. In all probability these leaf bases tapered abruptly outward during the first few centimeters and then only very gradually to the extreme tip of the leaf, as in modern cycads and large-leaved ferns such as *Cibotium*. Figures 13 and 19 may be taken then as representing the rachis<sup>5</sup> at a point some distance from the base of the leaf, and fig. 12 in turn may represent a distal secondary rachis or a tertiary one.

In the upper right portion of fig. 9 there is a localized group of a dozen or more conspicuous secretory canals scattered through, and inside of, the rind. With this exception, however, the petiole specimens referred to *M. Thompsonii* present a relative paucity of secretory canals. The lack is certainly more pronounced than in previously described species and compares closely with the similar negative feature of the leaf bases in organic connection with the stem.

One of our coal ball specimens contains a number of leaves of the *Alethopteris* type, most of which have been cut in transverse sections. Although there is considerable reason to believe that certain species of this genus were borne by the *Medullosas* it must be admitted that the present report does not further our knowledge of that relationship. However, certain features of these Iowa specimens do contribute toward a clearer understanding of their structure.

The restoration shown in pl. 13 is a composite drawing compiled from the best-preserved portions of a dozen or more leaflets. The coal ball containing the pinnules is highly pyritized, although that mineral has not penetrated the leaf tissues to any appreciable extent. Both peel preparations and ground sections proved unsatisfactory for photographic reproduction.

<sup>4</sup> It may be noted that the illustrations of these petiole and rachis fragments in transverse section are all reproduced at the same magnification. Although it necessitates considerable variation in figure size I believe that if this practice could be more generally adhered to it would greatly facilitate the distinction between different species as contrasted with the differences represented by the ordinal position of the leaf part represented.

<sup>5</sup> In view of the rather irregular dichotomy of the frond of *Alethopteris* and certain related species (Bertrand, '32) the term rachis is used here rather loosely to signify the larger proximal branches of the petiole.

Within the epidermis there is a clearly defined hypodermal layer and under this a third series of cells differing from the hypodermal in their vertical alignment. In all probability they were chlorophyllous in life, functioning as palisade cells.

The under-side of the leaflets presents a conspicuous combination of short papillose cells and long multicellular hairs. The cells densely cover almost the entire under-side, and in all probability the stomata were located among their swollen bases. It has not been possible to identify the guard cells. The elongate multicellular hairs are most striking (fig. 11). Most of them have been broken, but the few apparently entire ones consist of five or six cells. Within the epidermal papillae there is a zone of compact, more or less isodiametric, angular cells. The tissue between this and the palisade cells is very poorly preserved. However, I have observed that the region in close proximity to the central vein is occupied by loosely organized, horizontally arranged cells. There is no reason to believe that these did not extend to the margin of the leaflet as shown, although it should be noted that this feature of the restoration is uncertain. Nor has it been possible to distinguish with clarity the structure of the vascular tissue.

Sections of presumably Alethopterid leaves found associated with Medullosan petioles have been described and figured by Scott, '99, Steidtmann, '44, and Schopf, '39. Scott (p. 101) notes: "I have not yet found absolute proof that these leaflets belong to the '*Myeloxylon*' rachis, but the constancy of association, and general agreement in the structure leaves no real doubt." This opinion seems to be shared by Schopf and Steidtmann in their respective treatments of *M. distelica* and *M. Noei*.

The general similarity among the leaves illustrated by Scott and Steidtmann and our Iowa specimens lends support to this relationship with the *Myeloxylon* petiole remains. The distinctive multicellular hairs are illustrated in Steidtmann's specimens although these are not indicated in the English material. Nor is the hypodermal layer of cells indicated in Scott's fig. 17, although the preservation of his material apparently was rather inferior in this respect.

There is also a striking resemblance between the anatomy of the fossil leaflets and those of the living cycads (fig. 10). Assuming that the elongate spongy mesophyll cells are uniform through the width of the fossils the two are very nearly identical, with the exception of the multicellular hairs that are lacking in *Cycas revoluta*.

#### Roots.—

A number of isolated roots have been found in the Urbandale petrifications. Many of them compare closely enough with those described by Steidtmann ('44) and Schopf ('39) as to leave no doubt of their Medullosan affinities. It is not possible, however, to refer them with certainty to any species of the genus.

Most of the roots are tetrarch (fig. 15) and show various stages in the development of the secondary xylem. One is hexarch (fig. 16) although the stele is enclosed by a band of periderm characteristic of Medullosan roots.



*The Restoration* (pl. 13)—

The conspicuous role that the *Medullosas* evidently played in Pennsylvanian landscapes makes some sort of restoration of these plants desirable. Although the plant shown in pl. 13 is captioned "a *Medullosa* of the Anglorota group" it is based primarily on the stem and leaf remains of *M. Thompsonii*. However, aside from differences in size, there is no reason to believe that the Anglorota species presented any great dissimilarity in their general habit. In order that this restoration may bear no false implications or in any way convey impressions that do not rest on established facts the following points should be clearly understood: We do not know the exact height of any species of this group, but judging from the relatively small amount of supporting tissue they were probably not more than a few feet high,—perhaps 3–5 feet is self-supporting. If the plants attained greater heights let us assume up to 15 or 20 feet, it is likely that they grew in rather dense stands and supported one another, or relied upon the trees and shrubs of other species.

The fronds were large in proportion to the diameter of the stems, and in order to arrive at a reasonable approximation of their size, measurements have been made of ten living species of cycads as well as a species of *Cibotium* growing in the Garden greenhouses. In the cycads there is a rather constant ratio between the basal diameter of the petiole and the length of the leaf. However, *Alethopterid* leaves possessed a considerably higher breadth/length ratio than modern cycads, probably lying closer to that of a *Cibotium* frond. Yet from the structural similarity of the *Alethopteris* leaflets and those of a modern cycad it is certain that the weight of a *Medullosa* leaf, for its total area, was much closer to the cycads than a large-leaved fern. These points have been duly considered in determining the size of a *Medullosa* frond, relative to stem diameter, based on petiole diameter measurements.

As for the morphology of the leaves, indications are that the primary rachis gave rise to successive unequal bifurcations in at least some species of *Alethopteris* and related form-genera (Bertrand, '32, p. 67; Kidston, '11, fig. 7). It is reasonable to assume that the leaf size varied appreciably in the different species of the Anglorota group. Although the stem as shown in the restoration probably bore a crown of perhaps six to a dozen (more or less) leaves more precise detail could be shown if only one leaf were drawn in. Furthermore, the leaves were probably borne in a manner comparable with that of modern tree-ferns although the single leaf shown has been illustrated so as to conserve space and at the same time bring out the salient features of its construction.

Reproductive structures have been omitted from the drawing. Although seeds have been found on *Alethopteris* leaves (Halle, '29) and they are abundantly associated with the stems in the Iowa coal balls, it seemed best to postpone this feature of the restoration until further evidence is forthcoming.

*Diagnosis of Medullosa Thompsonii Andrews.*—

Stem approximately 3.6 cm. in diameter, epidermal cells radially elongated,



fibrous cortical strands circular to slightly elongated radially and anastomosing only at extended intervals, secretory canals rare in outer cortical (rind) region, internal periderm present; stelar system of three endocentric steles fusing upward, leaf trace sheaths poorly developed.

Petioles approximately 2.2 cm. in diameter at point of departure from stem, secretory canals not abundant.

Locality: Urbandale Coal Mine, Des Moines, Iowa.

Horizon: Pennsylvanian, Des Moines Series.

Type specimen: No. WCB420, Henry Shaw School of Botany, paleobotanical collections.

*Other Medullosan Stems.*—

Fragments of other stems, recognizable as belonging to the genus *Medullosa*, are included in our collection from the Urbandale mine. Although not sufficiently well preserved to merit specific recognition, one is worth a brief note. As shown in fig. 7 only the steles, of which there are two, are preserved. The periderm is sufficiently intact to indicate that no more than two were originally present. Aside from this, all extra-stelar tissues have been destroyed. The smaller stele measures 8.0 x 4.0 mm., and the larger 15.5 x 4.0 mm. although it is obviously crushed, probably nearer 15.5 x 6 mm. in life. Both are slightly endocentric, but this feature is much more pronounced in *M. distelica*, the only other known bistelar species. It is also appreciably smaller than *M. distelica* (see pl. 8), being more or less intermediate in size between that species and *M. Thompsonii*.

*Myeloxylon Bendixenii* sp. nov.

Included in the Medullosan petiole specimens from the Urbandale mine is one that is decidedly different from those described above as *Medullosa Thompsonii*. This petiole is large, as compared with the others, measuring approximately 3 cm. in diameter although it was somewhat compressed prior to fossilization (fig. 8). Since the most distinctive features lie in the structure of the rind a representative portion of this is shown in detail in fig. 35. Within the epidermis there is a band of parenchymatous cortex, 5–6 cells deep. This in turn encloses a broad and very conspicuous fibrous zone which averages nearly 2.0 mm. thick. The radial and tangential dimensions of the fiber bundles are more or less equal although many of them are quite irregular. A glance at fig. 8 reveals more in this respect than could be conveyed by many pages of measurements.

With the exception of the outermost strands almost every strand is associated with a secretory duct on its outer side (fig. 35). These ducts average 190  $\mu$  in diameter.

As may be noted in fig. 8, there are a few fibrous strands scattered deep within the petiole. The secretory ducts, with their conspicuous black contents, are also numerous in the ground parenchyma scattered among the vascular bundles. The large size of this petiole, as well as the anatomical details of the rind, leaves little doubt that it is not to be associated with *Medullosa Thompsonii*. Thus, until more

stem remains are retrieved from Iowan petrifications it must be referred to *Myeloxylon*.

A comparison with other American species reveals no close alliance with previously described specimens. Penhallow's *Myelopteris* (*Myeloxylon*) *topekensis* (Penhallow, '97) is not sufficiently well preserved to allow comparison. Arnold and Steidtmann ('37) proffered the same opinion concerning this species, and there seems to be no justification for further reference to it in the literature, since its exact origin is also not known.

*Myeloxylon Bendixenii* differs from both *M. missouriensis* Arnold & Steidtmann ('37), and *M. zonatum* Steidtmann ('44) in the following respects: the rind of *M. Bendixenii* is twice as thick; secretory canals are much more abundantly associated with the fibrous strands; and the inner border of the rind is not as sharply delimited.

*Diagnosis of Myeloxylon Bendixenii* Andrews.—

Petiole large (3 cm. diam.), parenchymatous cortex 5–6 cells deep between epidermis and rind, rind (fibrous zone) 2 mm. thick radially, fiber bundles more or less isodiametric in transverse section, almost every bundle accompanied by a secretory duct on outer side, ducts averaging 190  $\mu$  in diameter.

Locality: Urbandale Coal Mine, Des Moines, Iowa. (see p. 323.)

Horizon: Pennsylvanian, Des Moines Series.

Type specimen: No. WCB429, Henry Shaw School of Botany, paleobotanical collections.

This species is named in honor of Charles Shuler Bendixen, an official of the Shuler Coal Mine, located eight miles west of Des Moines, Iowa.

*Schoptiastrum decussatum*, gen. et sp. nov.

The following description is based on two stem fragments also found in coal balls from the Urbandale mine near Des Moines. Although much remains to be learned of the plant as a whole the available information indicates a pteridosperm with strikingly distinct anatomical features, particularly the structure and arrangement of the leaf traces. It is intended that this paper serve only as a preliminary report to be supplemented by a full account when more complete specimens are forthcoming. Of the two specimens at hand, one (WCB434) consists of a decorticated stele, and another (WCB421) in which both stele and outer cortex are preserved.

Judging from the more complete specimen (fig. 17) the stem was about 21 mm. in diameter. The specimen illustrated (measuring 9. x 30. mm.) appears collapsed due to decay of the internal cortical tissues. However, there is no reason to believe that the stem was not cylindrical or nearly so in life.

The primary wood is rather sharply 4-angled in transverse section, measuring 2. mm. on a side, and is composed of elongate tracheids with some interspersed parenchyma. The infiltrations of pyrite, as well as occasional cracks (fig. 18), have destroyed a few of the cells. The parenchyma cells were relatively few, far

less than in pteridosperm stems (presumably the most closely related to this genus) such as *Rbetinangium* and *Heterangium*.

In both their structure and order of departure from the stele the leaf traces differ in striking fashion from any other stem that has been referred to the Pteridospermeae. In the stem shown in fig. 17 it may be noted that, although the primary xylary tissues are crushed, the two leaf traces appear to be diametrically disposed, that is, 2-ranked. This opposite arrangement is confirmed in the other specimen (WCB434) in which the primary wood is somewhat better preserved (fig. 18).

At the earliest observed point in its departure from the stele the trace is already bilobed (fig. 18, lt<sub>2</sub>) and its cross-sectional size is equal to fully half that of the cauline primary xylem. Even at this level, however, each lobe has in turn started to divide, there being four exarch protoxylem groups in the trace. Reason for believing that these four originated from two exarch groups in the primary stele will be given below. In following this leaf trace through the length of the specimen (3 cm.) very little change takes place, but the opposite trace, as well as the one shown in fig. 17 (from specimen 421), reveals at least some of the subsequent changes. The trace as a whole becomes strongly 4-lobed and tangentially elongate with the protoxylems occupying the outermost tip of each lobe. Shortly prior to its departure from the stele the protoxylem groups in the distal lobes of the trace divide (fig. 18, pxt). It is not known whether further lobing or actual division occurs in the traces at a higher level.

Judging from the difference in the structure of a pair of traces at any one point, it is evident that one departed appreciably in advance of the other. The origin of the succeeding pair of traces may next occupy our attention. In two of the ground sections prepared from specimen 434, four exarch protoxylem groups are clearly defined in the stele. These are paired, and alternate with the leaf traces, as shown in fig. 18, pxs. It seems most probable that the next pair of traces will have their origin from these protoxylem points, although confirmation of this must await the discovery of longer stem fragments.

Judging from these opposite pairs of protoxylem groups, an individual trace started with but 2. Shortly following segregation of the trace from the primary stele of the stem each protoxylem divided, resulting in 4, and this was then followed by the lobing of the traces as a whole into 4 parts.

As the traces increased in their tangential dimensions in passing through the secondary wood they left a broad gap in that tissue and a small quantity of secondary wood accompanied the trace on its outer face (fig. 22, x 2).

The secondary xylem of the stem is strongly developed, attaining a maximum radius of nearly 3 mm. The shape of the tracheids as seen in transverse section is of the irregular angular type found in other pteridosperm stems (Andrews, '40, p. 89) such as *Lyginopteris* and *Medullosa* (Anglorota section), and their radial walls are covered with closely compacted angular bordered pits. The same type of pitting is also found in the metaxylem tracheids.

The outer cortex is constructed of thin longitudinal-radial plates of fibers

(fig. 20) rather regularly spaced with parenchymatous cells. Although the latter vary appreciably in size most of them are characteristically elongated ( $140. \times 80. \mu$ ) in a tangential direction. The fibrous strands anastomose only at extended intervals, appearing in tangential section (fig. 21) as nearly parallel strands. This fibrous zone of the cortex is separated from the epidermis, the cells of which measure  $35. \times 20. \mu$ , by a single row of cortical parenchyma cells considerably smaller than those deeper within.

*Diagnostic Summary of the Genus Schopfiastrum.*—

Outer cortex composed of nearly parallel radial-longitudinal fibrous strands separated by tangentially elongated parenchyma cells; secretory canals absent or very rare; primary xylem a mixed protostele, protoxylem exarch, two opposite pairs present in internodes; leaf traces large, soon becoming bilobed and accompanied at least to the inner cortex by a small amount of secondary wood; traces arranged in opposite pairs, one of each pair departing ahead of the other, the succeeding pair of traces alternating; secondary wood present, with closely compacted, reticulate-bordered pits on radial walls of tracheids.

Locality: Urbandale Coal Mine, Des Moines, Iowa.

Horizon: Pennsylvanian, Des Moines Series.

Type specimens: Nos. WCB421 and WCB434, Henry Shaw School of Botany, paleobotanical collections.

The genus is named for Dr. James M. Schopf, of the United States Bureau of Mines, in recognition of his contributions to Carboniferous paleobotany.

*Discussion.*—

The genus *Schopfiastrum* is considered referable to the Pteridospermeae in view of the characteristic fibrous outer cortex, the structure of the leaf traces which compares in a general way with that of *Rbetinangium* and *Heterangium*, and the closely compacted reticulate pitting of the tracheids as well as their shape as observed in transverse section.

The closest affinities of *Schopfiastrum* seem to lie with the genera *Rbetinangium* and *Heterangium*. In fact, during the earlier phases of this investigation the stem was tentatively considered as a new species of *Rbetinangium*. However, when the structure of the primary xylem and the organization of the traces had been worked out this treatment was found to be quite untenable. The outer cortex is very similar to that of *Rbetinangium arberi* Gordon ('12), both possessing the distinctive tangentially elongated parenchyma cells between the fibrous strands. However, *Schopfiastrum* lacks the secretory canals, with their radially arranged epithelial parenchyma, which are present in the outer cortex of *Rbetinangium*. A few apparent canals have been observed in this region but in almost all cases they are clearly the result of fungous or bacterial action. The leaf traces of the Iowa stem are comparable with those of *R. arberi*, in their massive size and exarch protoxylems but the comparison goes no further. In *Rbetinangium* the trace is composed of a number of irregularly U-shaped strands interspersed with

parenchyma, quite different from the predominantly tracheidal unit traces of *Schopfiastrum*.

There is no evidence in the Iowa stem of horizontal sclerotic plates in the inner cortex such as are found in *Heterangium*. The single leaf trace (to each petiole) of *Schopfiastrum* precludes any close relationship with the polydesmic *Heterangium* and differs markedly in size, form, and arrangement from any of the *Eu-heterangium* species.

*Schopfiastrum* is of special interest not only in its clearly defined generic characters, but, judging from the structure of the primary wood, it is a rather primitive pteridosperm. As stated above, it seems to lie as close to *R. arberi* as any described pteridosperm yet the protosteles of *Schopfiastrum*, its less complex leaf traces, and the lack of secretory canals in the cortex, all point toward a less specialized plant. Also, the monotypic *Rhetinangium* was found in the middle Lower Carboniferous of Scotland while *Schopfiastrum* is of much more recent origin, coming from middle Upper Carboniferous rocks. This is an apparent paradox that is by no means unique in paleobotany and at least offers assurance that there are many more unknown species and genera in the Seed-fern group that remain to be found.

#### Appendix I.

The late Professor A. C. Noé is quite justly acknowledged as having been the first person to collect coal balls in this country, nearly 25 years ago, and to him is due most of the credit for initiating interest in their study. However, Mr. F. O. Thompson has recently brought to my attention a point of historical interest pertaining to an earlier discovery of coal balls in America that seems worth mentioning.

In Volume II of the Iowa Geological Survey Reports Dr. C. R. Keyes ('94) reported the presence of coal balls (although they were not described under that name) in the Bloomfield mine near Des Moines. To quote directly from this account:

Associated with the coal bed are numerous lenticular masses of ironstone. They vary in size from a few inches to ten or twelve feet horizontally, and up to six feet vertically. The smaller ones are commonly called "nigger heads." These segregations occur in all parts of the coal seams, but they are most abundant in the roof and upper surface of the coal, where they are often so close together as to form an almost continuous layer. It is common for the nodules in the upper part of the coal to project upwards above the top of the seam, often two to three feet in case of the large masses. They are covered usually by a few inches of carbonaceous material. [pp. 279-281].

In the Annual Report for 1896 A. F. Bain ('97) reported the presence of "clay-ironstones" in the Bloomfield mine and several others, and he notes that: "An analysis of similar material from a mine in Mahaska County showed the presence of about 88 per cent of limestone, with 8 per cent of organic matter and small percentages of iron oxides and sulphides." (p. 297)

The authors in both instances figure vertical sections through the coal showing the coal balls ("ironstones") in the upper portion of the seams. Thus there is no



possibility of their being confused with the sterile slate-gray concretions common in the overlying shales, and also referred to by the miners as "nigger heads." The presence of 8 per cent organic matter removes any doubt as to their identity, and the high percentage of limestone reported by Bain also suggests coal balls of fine quality. At least his figures leave little room for the obnoxious iron sulphide.

These petrifications, although apparently well known to geologists, did not reach the hands of paleobotanists until a quarter of a century later when Noé started collecting in Illinois.

#### Appendix 2.

*Medullosa anglica* var. *thiesseni* was described by Schopf in 1939 although at that time its origin was unknown beyond the knowledge that it had been collected in the "western coal fields of this country." The horizon from which var. *thiesseni* came has now been established and the information is presented here, with Dr. Schopf's permission, in order that the record of the western *Medullosas* may be as complete as possible.

The specimens upon which Schopf's ('39) description were based were found by R. V. Pepperberg in southeastern Nebraska in 1907. Three years later Pepperberg described a Carboniferous flora, in which *Neuropteris* predominated, from two localities, one near Nebraska City (Otoe Co.) and the other near Peru (Nemaha Co.). It is not clear at which locality the specimens were found but the horizon is believed to be the same. The specimens are mentioned on p. 330 (Pepperberg, '10) in a letter addressed to him by David White. The generic identity of the specimens was established by Reinhardt Thiessen, for whom they were later named.

In 1936 Pepperberg's collections were referred to by Elias ('36) as follows:

19. Near the top of the Table Creek shale formation. The well-preserved flora, collected in soft sandy shale 1½ feet below the Dover limestone, contains *Neuropteris* and *Annularia*. Probably from this horizon came the flora consisting of numerous *Neuropteris* leaves and *Calamites* stems in sandstone and sandy shales at Brownville, Nemaha County, Nebraska . . . and at Nebraska City, Otoe County, Nebraska (7, p. 313).<sup>6</sup>

In 1943 Condra and Reed reported that "the so-called 'Table Creek shale' represents three formations, i. e., the shale below the Dover (with the Maple Hill limestone missing), plus the sandstone equivalent of the Tarkio, plus the Willard shale." In the stratigraphic column given by Condra and Reed (p. 42) the "Table Creek" is from the lower part of the Richardson sub-group. The latter is the upper sub-group of the Wabaunsee group which is the uppermost part of the Virgil series.

It is of considerable interest to find a *Medullosa* of the Anglorota group from such a high horizon. All of the English species were derived from the Lower Coal Measures, well down in the lower part of the Pennsylvanian. The American *M. distelica* and *M. Thompsonii* likewise are from horizons considerably below the Table Creek shale. Thus it is evident that the *Medullosas* of the *anglica* type were not only widely distributed geographically but that this racial life span extended over many millions of years.

<sup>6</sup>This is a reference to Pepperberg's 1910 paper.



*Acknowledgment.*—

The addition of this chapter to American coal ball studies has been made possible through a gift from Mr. Frederick O. Thompson of selected specimens from his own collections. For his generous support and continued interest in the scientific progress of the investigation we are profoundly grateful. Thanks are also due Mr. R. M. Kosanke for the loan of slides of *Medullosa anglica* var. *thiesseni* from the collections of the Illinois Geological Survey; and to Mr. F. Tracy Hubbard for the loan of Iowa coal ball slides from the Botanical Museum of Harvard University. I am indebted to Dr. James M. Schopf, The United States Bureau of Mines, for many helpful suggestions pertaining to the taxonomy of *Medullosa*.

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## EXPLANATION OF PLATE

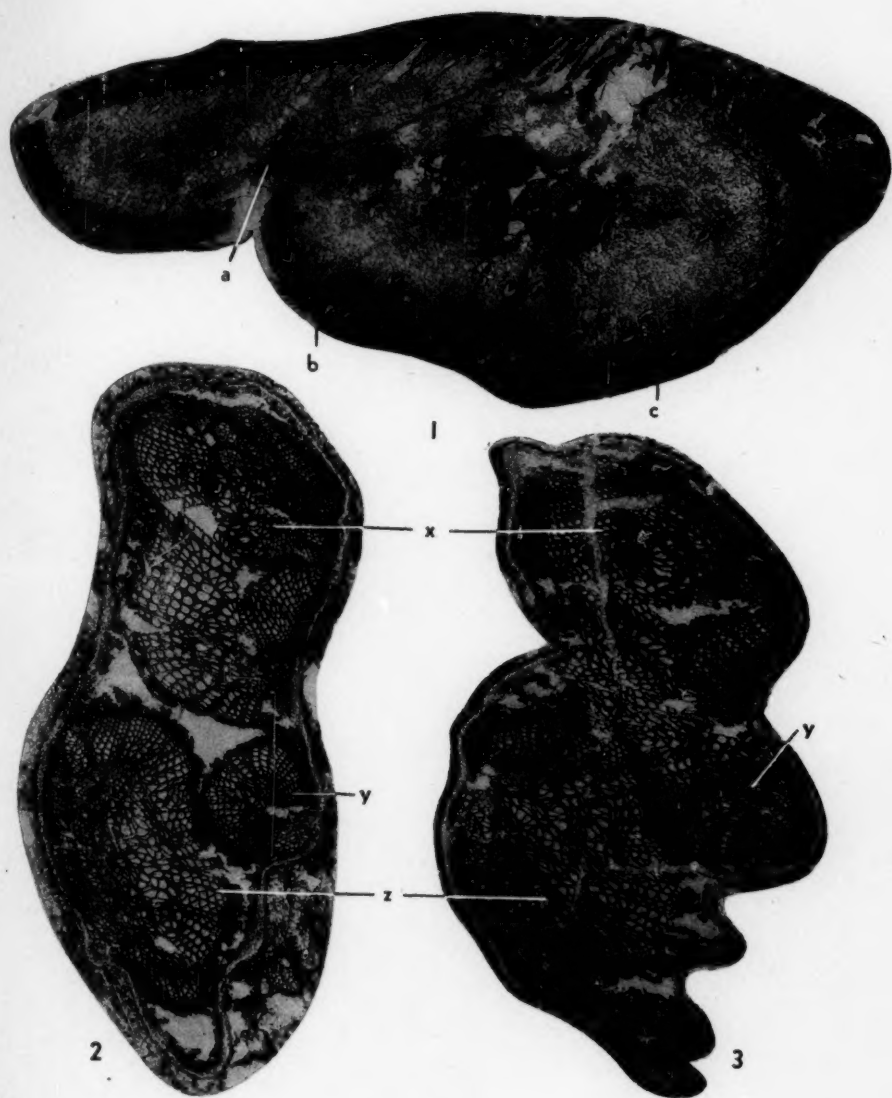
## PLATE 5

*Medullosa Thompsonii* Andrews

Fig. 1. The stem in transverse section showing a leaf trace departing at the left. *a*, fibrous strands separating stem from leaf base; *b*, *c*, between these two points the cortical rind is lacking, explanation in text. WCB420-2-A3, x 2.3.

Fig. 2. Stelar system from fig. 1 shown at a higher magnification. *x*, *y*, *z*, steles. WCB420-2-A3, x 7.0.

Fig. 3. Showing fusion of the three steles. WCB420-1-A3, x 7.0.

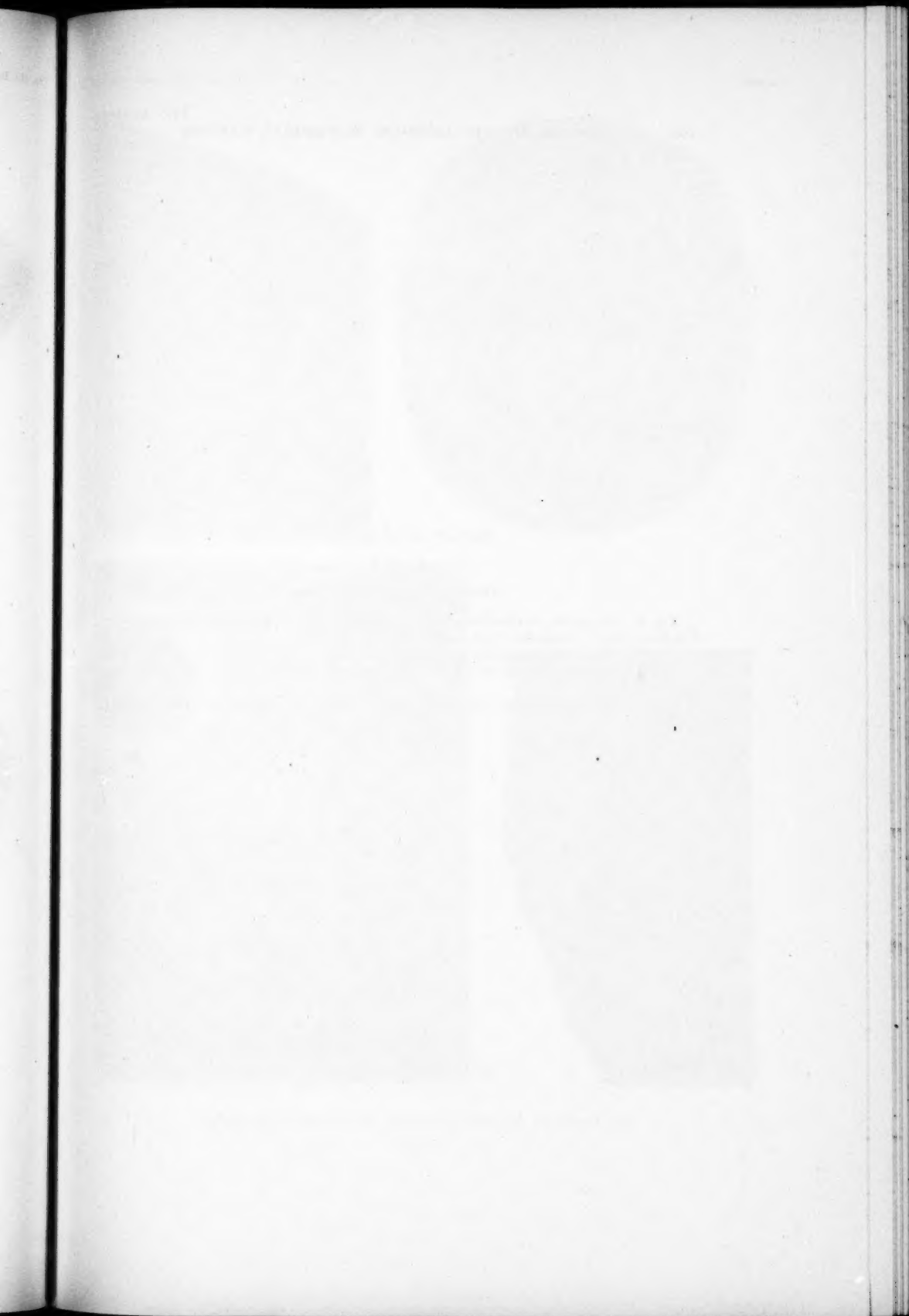


ANDREWS-AMERICAN CARBONIFEROUS FLORAS. VII

THE JOURNAL OF THE AMERICAN MEDICAL ASSOCIATION



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## EXPLANATION OF PLATE

## PLATE 6

*Medullosa Thompsonii* Andrews

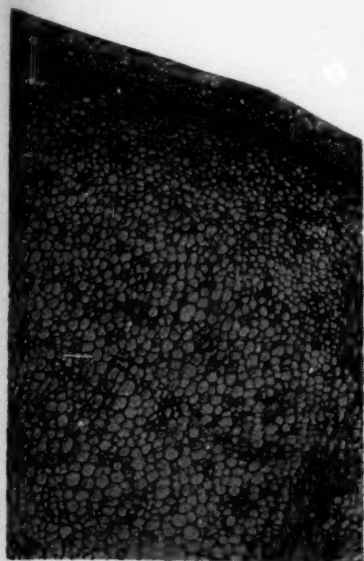
Fig. 4. Transverse section through outer cortex as that tissue appears between points *b* and *c* of fig. 1. Slide No. 1363, x 17.5.

Fig. 5. The rind or outer cortical fibrous tissue of the stem. Slide No. 1364, x 17.5.

Fig. 6. A single vascular bundle from the petiole shown in fig. 9. WCB426, Slide No. 1368, x 76.

Fig. 7. *Medullosa* sp. A bistelar Medullosan stem. Explanation in text. WCB461, x 4.2.

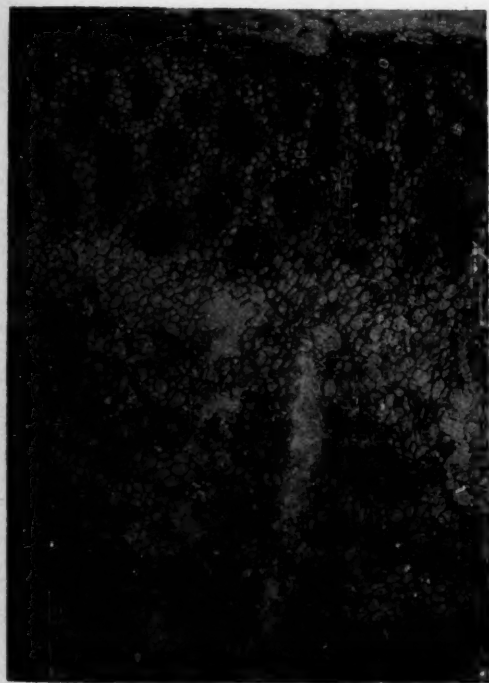




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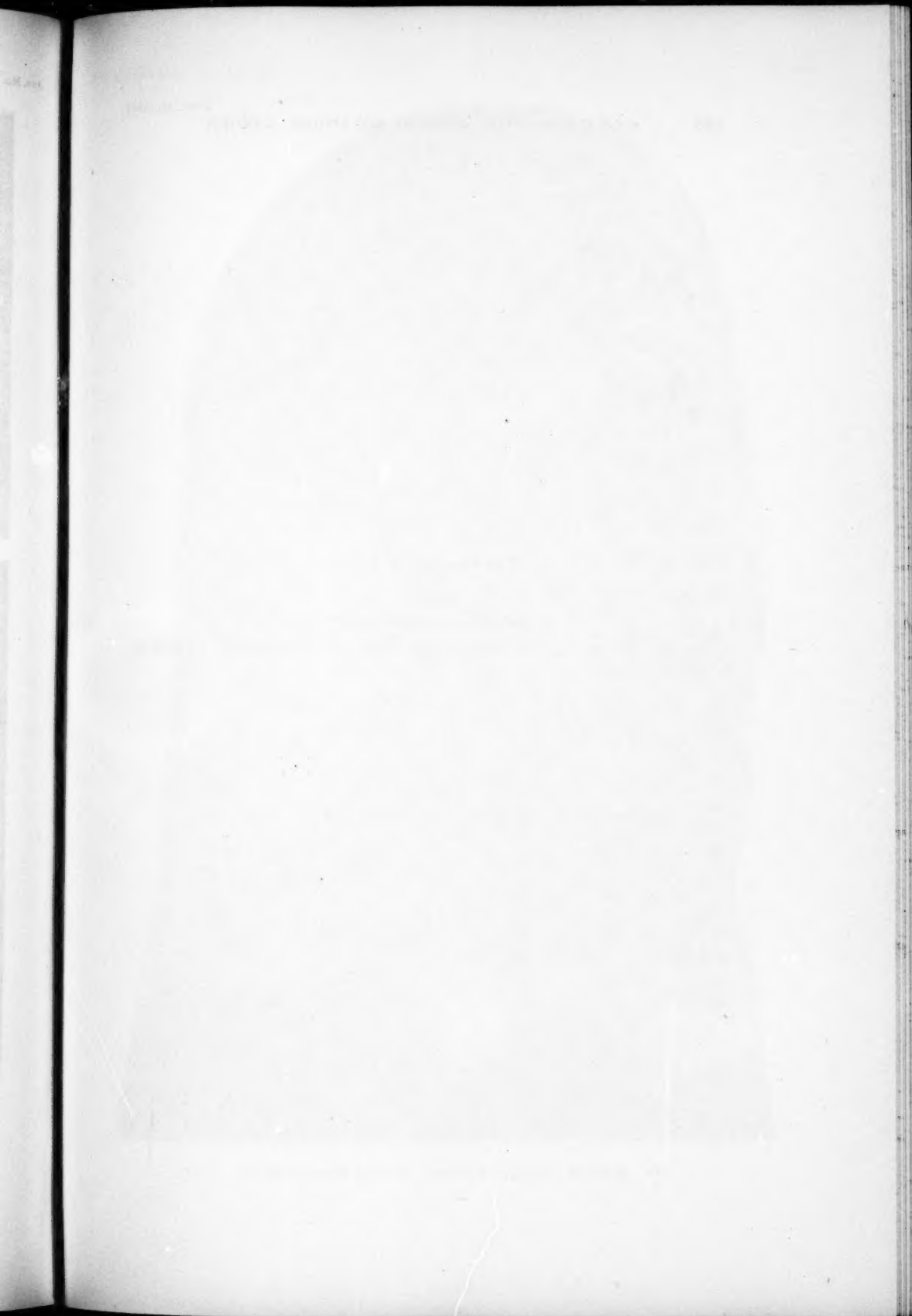
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ANDREWS-AMERICAN CARBONIFEROUS FLORAS. VII





## EXPLANATION OF PLATE

## PLATE 7

*Myeloxylon Bendixenii* Andrews

Fig. 8. Transverse section showing the greater part of the petiole. WCB429-S2,  
x 10.2.



8

ANDREWS-AMERICAN CARBONIFEROUS FLORAS. VII



AMERICAN-AMERICAN CARBONITE REFINERY





## EXPLANATION OF PLATE

## PLATE 8

*Medullosa Thompsonii* Andrews

Fig. 9. An isolated petiole believed to be referable to the stem species shown in fig. 1.  
WCB426-T2, x 10.2.

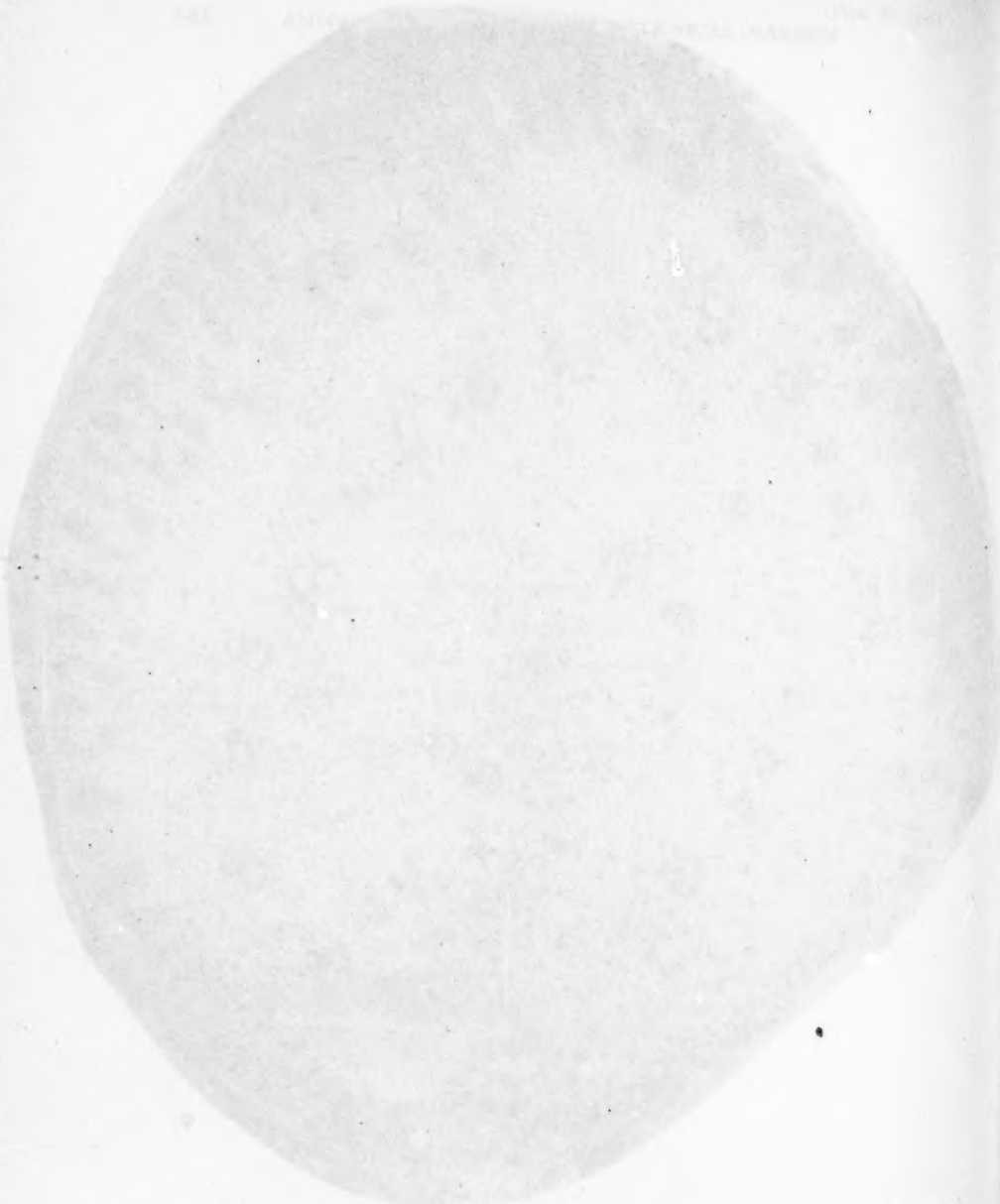


ANDREWS-AMERICAN CARBONIFEROUS FLORAS. VII

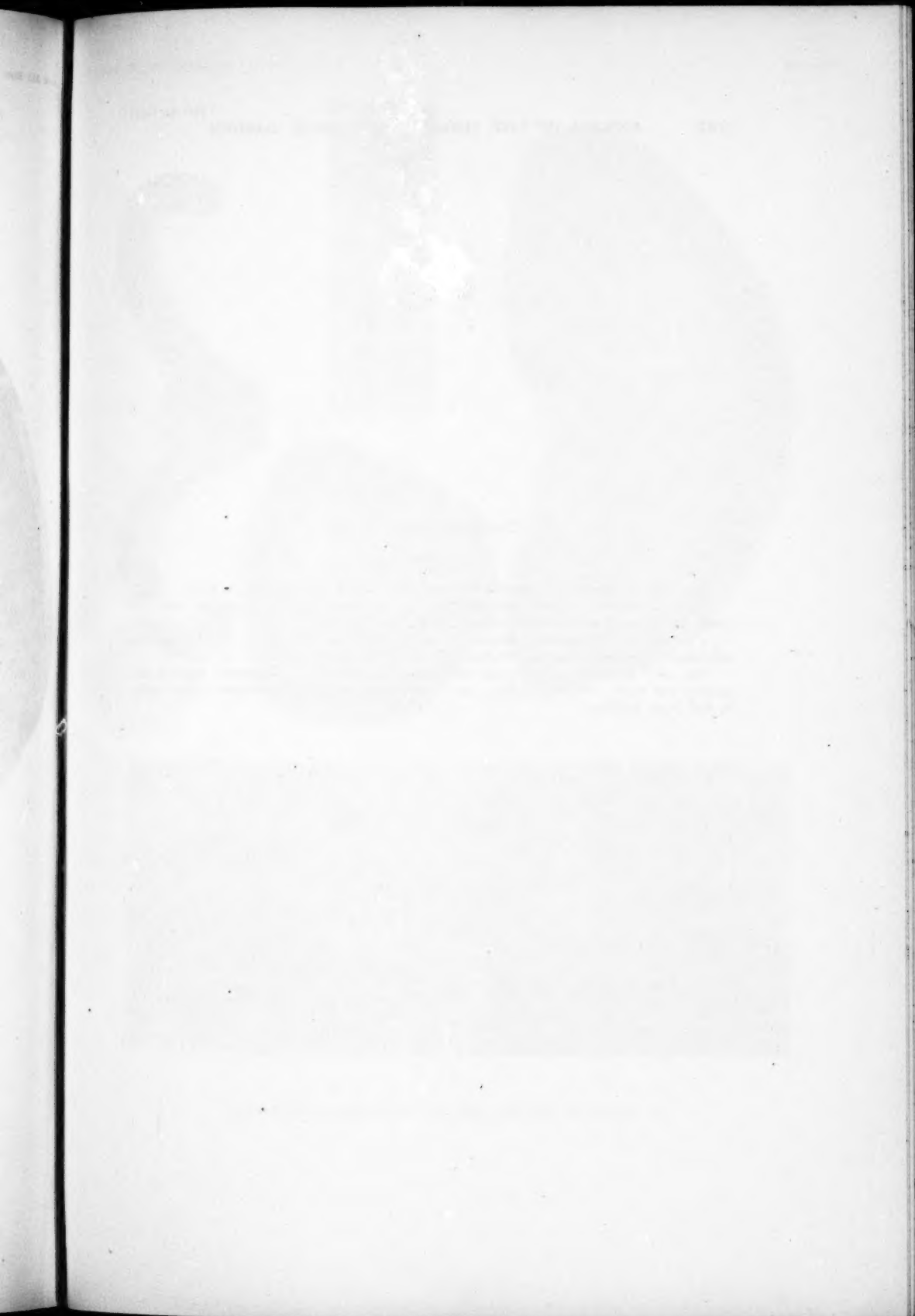
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## EXPLANATION OF PLATE

## PLATE 9

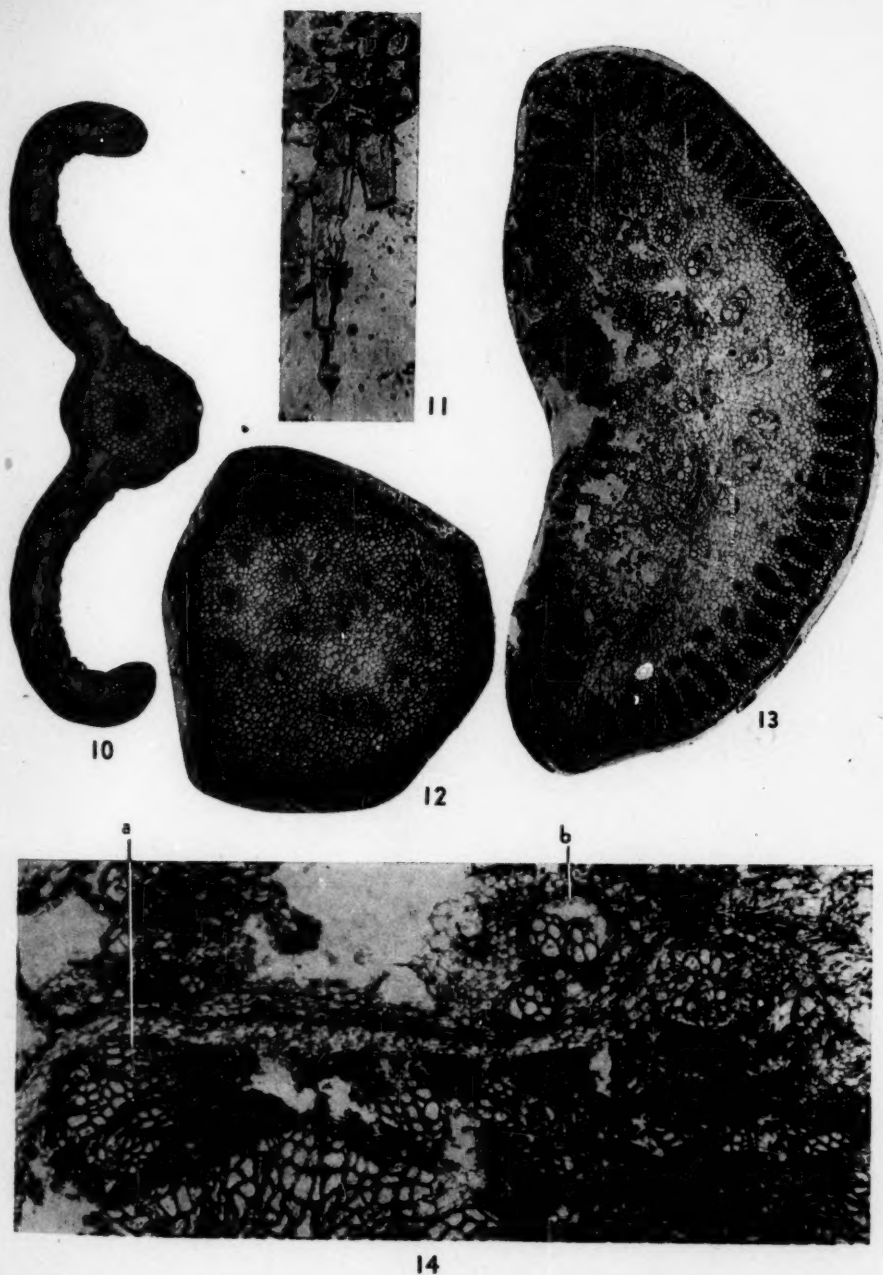
Fig. 10. Transverse section of a leaflet of the living *Cycas revoluta*, x 20.2.

Fig. 11. Showing a large multicellular hair, and basal portion of another, from the lower epidermis of an *Alethopteris*-like leaflet. Slide No. 1369, x 99.

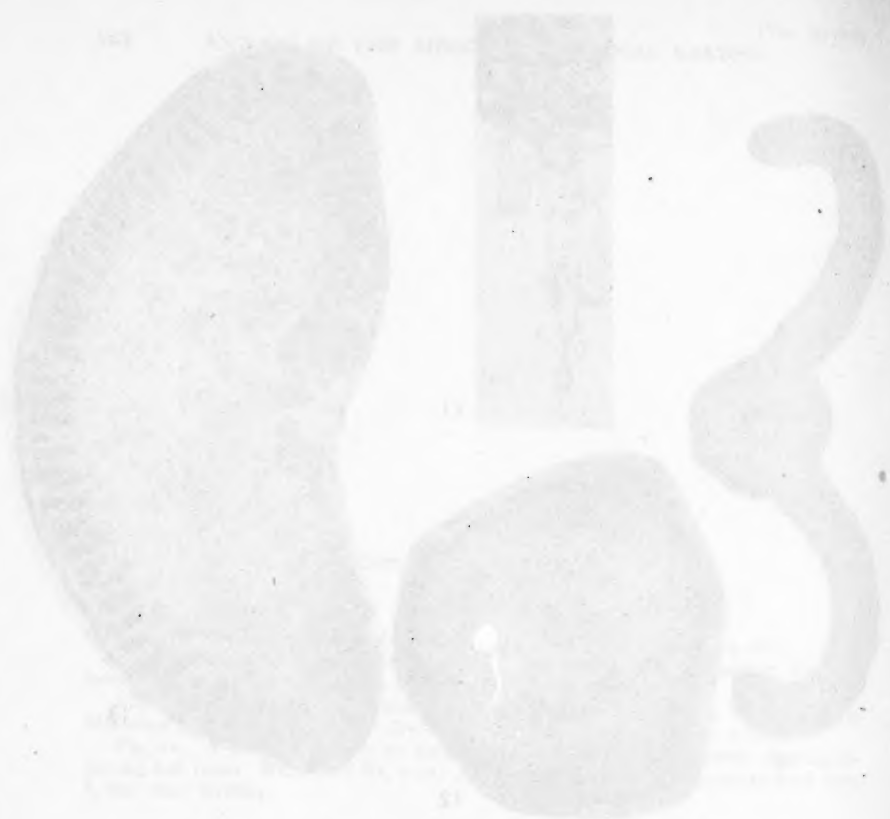
Figs. 12, 13. Transverse sections of rachis branches believed to be referable to *Medullosa Thompsonii*: fig. 12, WCB433-T1, x 11; fig. 13, WCB429-S2, x 10.2.

Fig. 14. A portion of the outer stelar region of *Medullosa Thompsonii*, showing departing leaf traces. WCB420-2-B3, x 22: *a*, leaf trace shortly after departure from stele; *b*, leaf trace dividing.





ANDREWS-AMERICAN CARBONIFEROUS FLORAS. VII





## EXPLANATION OF PLATE

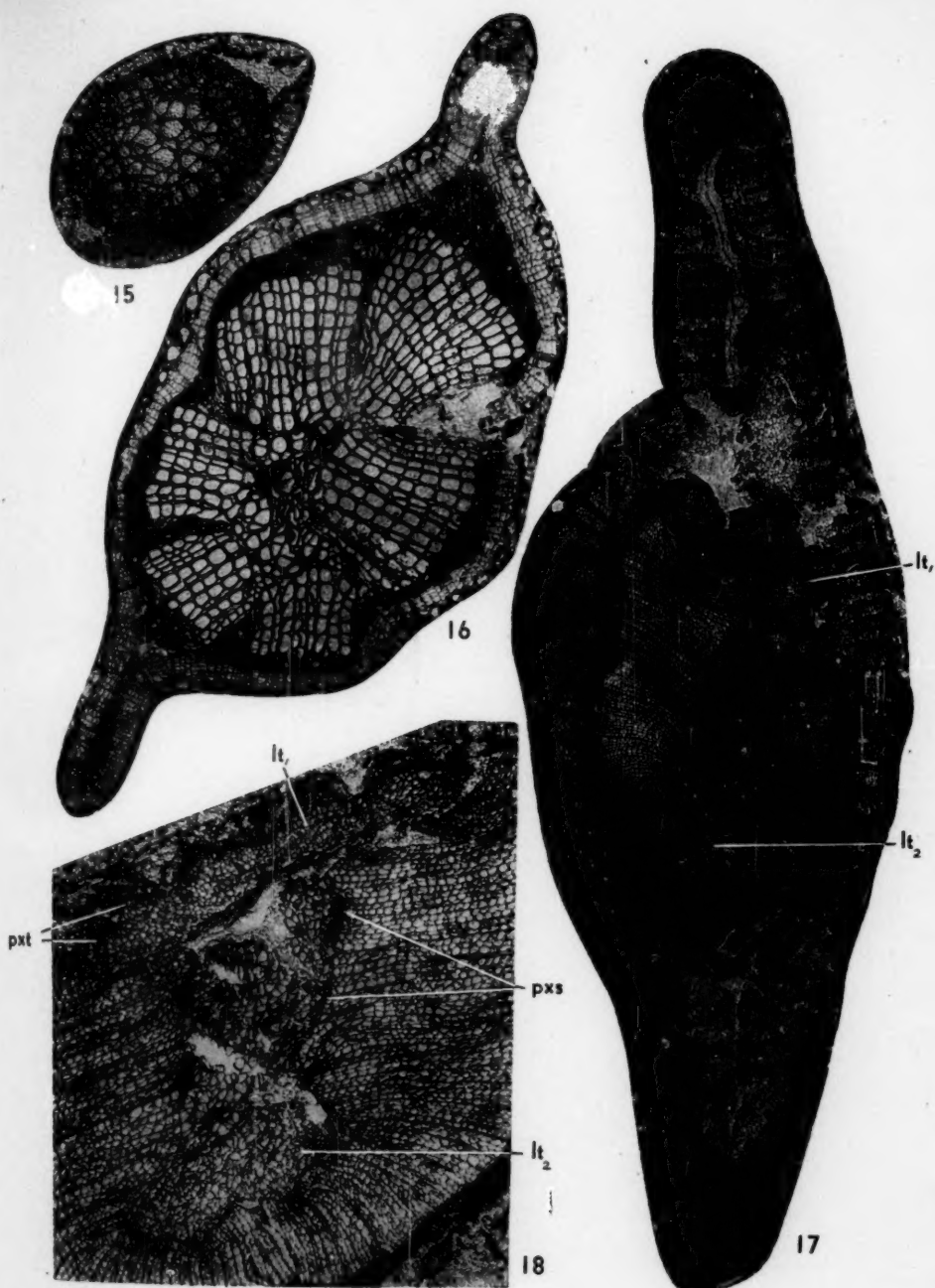
## PLATE 10

Figs. 15, 16. Roots found in coal balls associated with the Medullosan stems: fig. 15. WCB462, x 14; fig. 16. WCB422, x 14.

*Schopfiastrum decussatum* Andrews

Fig. 17. Entire stem in transverse section:  $lt_1$  and  $lt_2$ , leaf traces. WCB421, x 6.5.

Fig. 18. Showing central portion of stem (from another specimen) at a higher magnification:  $lt_1$ ,  $lt_2$ , leaf traces; pxs, protoxylem groups of stele; pxt, protoxylem groups of trace. WCB434. Slide No. 1353, x 11.



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## EXPLANATION OF PLATE

## PLATE 11

Fig. 19. Transverse of rachis branch believed to be referable to *Medullosa Thompsonii*. WCB427,  $\times 10.2$ .

*Schopfiastrum decussatum* Andrews

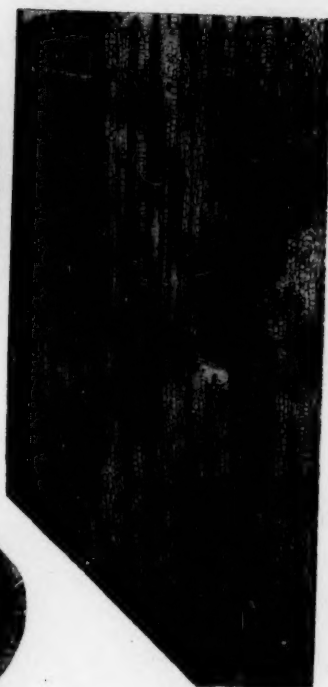
Fig. 20. The outer cortex in transverse section. Slide 1359,  $\times 37.5$ .

Fig. 21. The outer cortex in tangential section. WCB421-B-S4,  $\times 8.5$ .

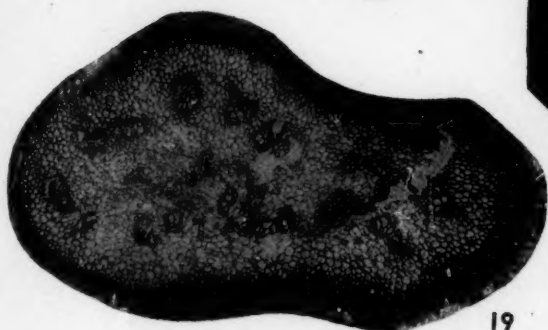
Fig. 22. Leaf trace departing from stele. This is a higher magnification of  $lt_1$  in fig. 17;  $\times 18.5$ .



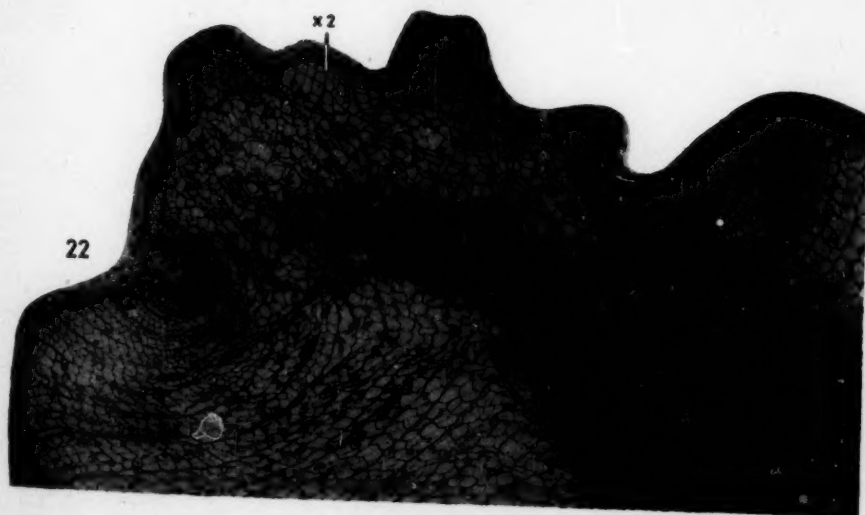
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21



19



22



Fig. 10



Fig. 11



Fig. 12



Fig. 13

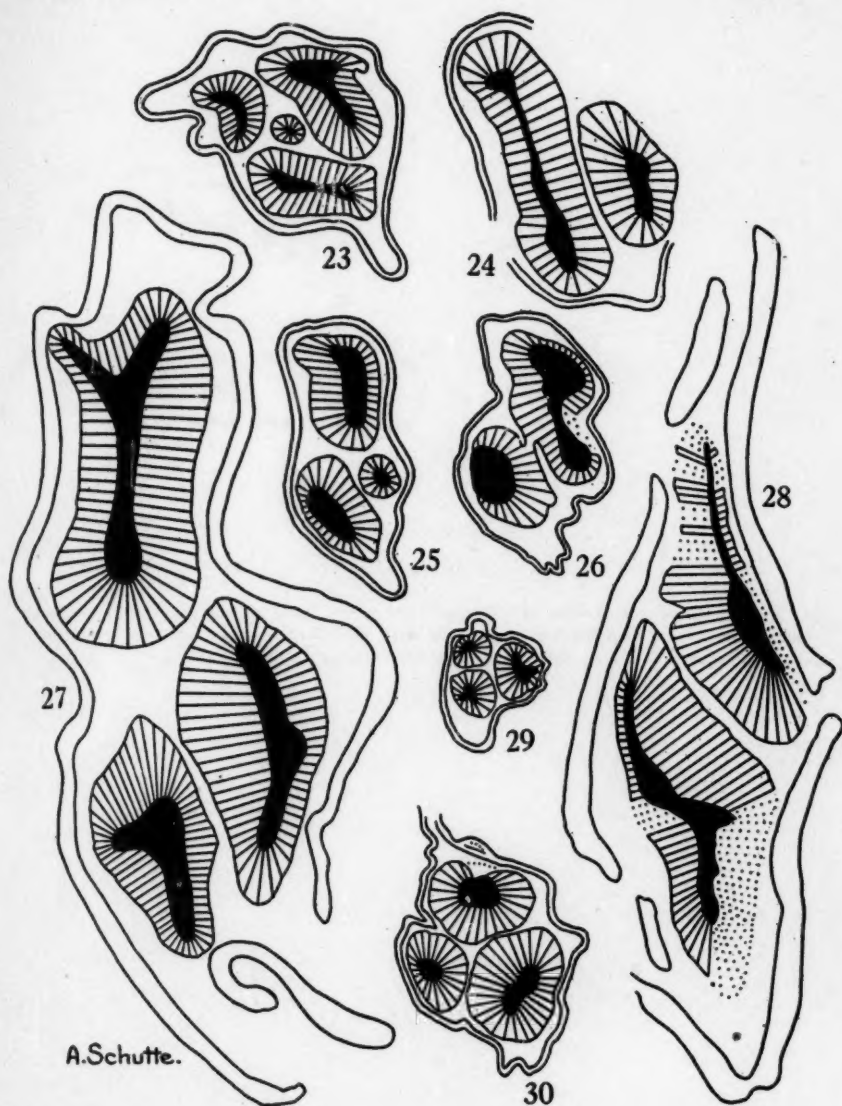
THE HOUSE OF REPRESENTATIVES  
OF THE STATE OF NEW YORK  
IN SENATE,  
January 10, 1901.

## EXPLANATION OF PLATE

## PLATE 12

Diagrams of the periderm and stelar systems only of the closely related species of *Medullosa* referable to the sub-genus *Anglorota*. The periderm is indicated by the enclosing, or partially enclosing, double line, the primary xylem in solid black, and the secondary xylem by radiating lines. *The magnification is  $\times 2.8$  in all cases.* Fig. 23. *M. centrofilis* De Fraine; fig. 24. *M. sp.* (see page 335); figs. 25, 26. *M. Thompsonii* Andrews; fig. 27. *M. anglica* Scott; fig. 28. *M. distelica* Schopf; fig. 29. *M. pusilla* Scott; fig. 30. *M. anglica* var. *thiessenii* Schopf.





AMERICAN CARBONIFEROUS FLORAS. VII

## EXPLANATION OF PLATE

## PLATE 13

Restoration of a *Medullosa* of the Anglorota group, based primarily on the stem and rachis remains of *M. Thompsonii*, together with associated foliage and root fragments. For further explanation see pp. 332, 334; x approximately 1/8.



ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VII.

## EXPLANATION OF PLATE

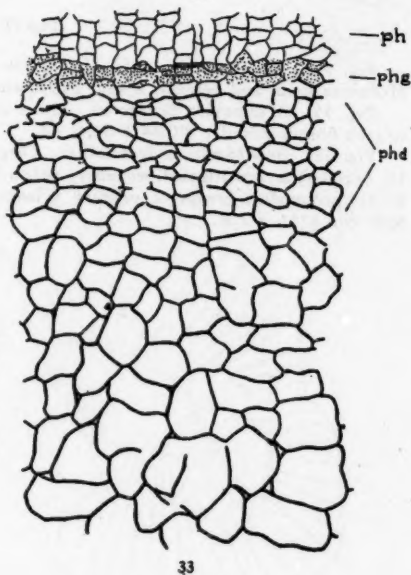
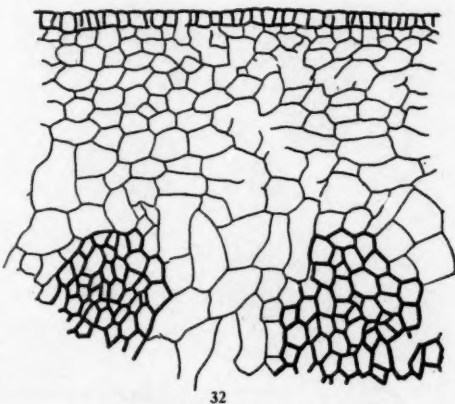
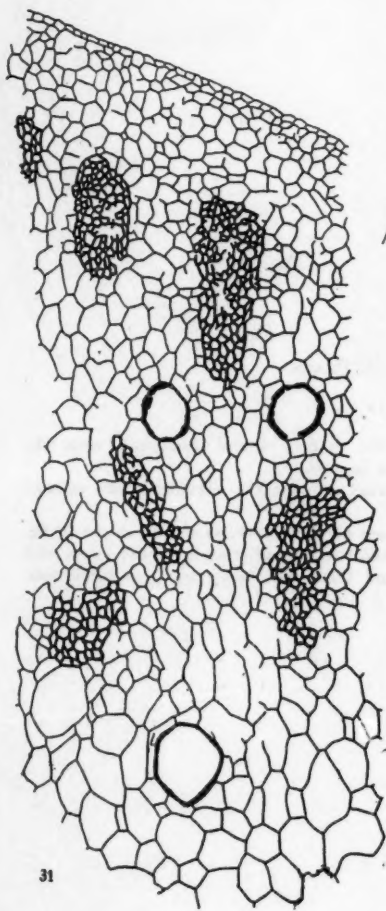
## PLATE 14

*Medullosa Thompsonii* Andrews

Fig. 31. Outer cortex of the petiole shown in fig. 9. WCB426-T2, x 36.

Fig. 32. Outermost cortex and epidermis of the stem shown in fig. 1. A part of two fibrous strands are also shown. Slide No. 1364, x 65.

Fig. 33. Cortex of the stem as it appears between points *b* and *c* of fig. 1: ph, phellem; phg, phellogen; phd, phelloderm. Slide No. 1363, x 65.



## EXPLANATION OF PLATE

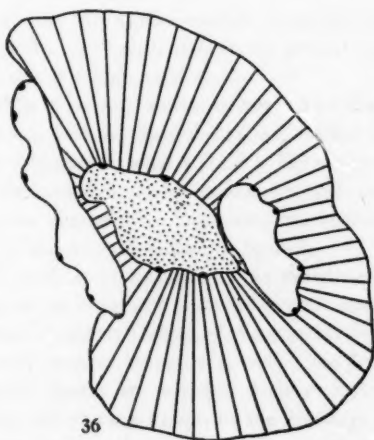
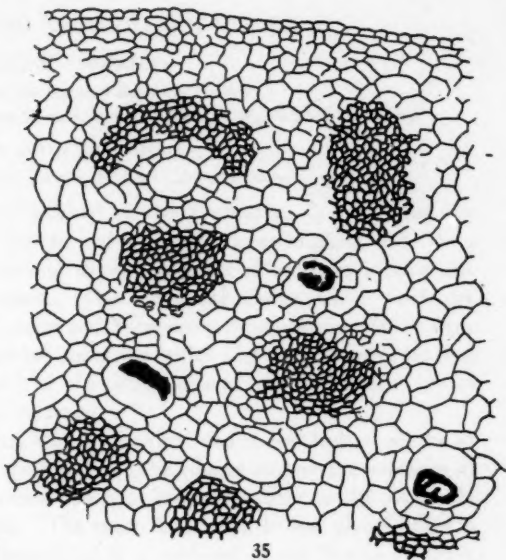
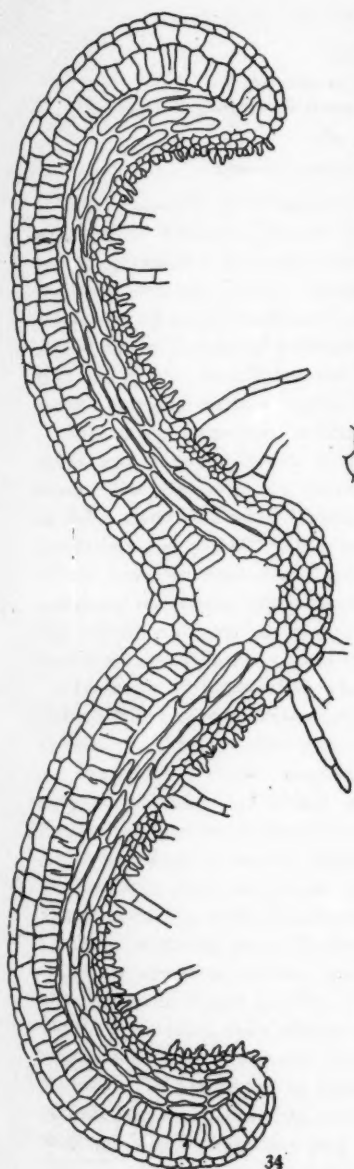
## PLATE 15.

Fig. 34. Reconstruction of *Alethopteris*-like leaflets found associated with the *Medullosa* stems and petioles, x 48. Explanation in text.

Fig. 35. *Myeloxylon Bendixenii*. Outer cortex showing the secretory canals exterior to each fibrous strand. WCB429-S2, x 42.

Fig. 36. *Schopfiastrum decussatum*. Diagram of the transverse section shown in fig. 18. Primary xylem stippled, secondary xylem indicated by radiating lines, and traces solid white; protoxylem groups of primary xylem and traces are shown by large black dots. Slide No. 1353, x 7.5.







BY MARY HARRINGTON AND OTHERS

## MAIZE IN THE YANHUITLAN CODEX

EDGAR ANDERSON

*Geneticist to the Missouri Botanical Garden*

*Engelmann Professor in the Henry Shaw School of Botany of Washington University*

AND JOHN JAY FINAN

*Research Assistant, Pioneer Hi-Bred Corn Company*

The appearance of a definitive edition<sup>1</sup> of the Yanhuítlan Codex, under the editorship of Wigberto Jimenez Moreno and Salvador Mateos Higuera, gives us a unique opportunity to learn something about the maize of southern Mexico immediately after the Spanish Conquest. This interesting Codex, which fascinates scholars by its naive blending of native and European techniques, provides us with a good deal of incidental information about the yields and uses of maize at that time and place. In addition, some of the delineations of the maize plant are so realistic as to be useful scientific evidence.

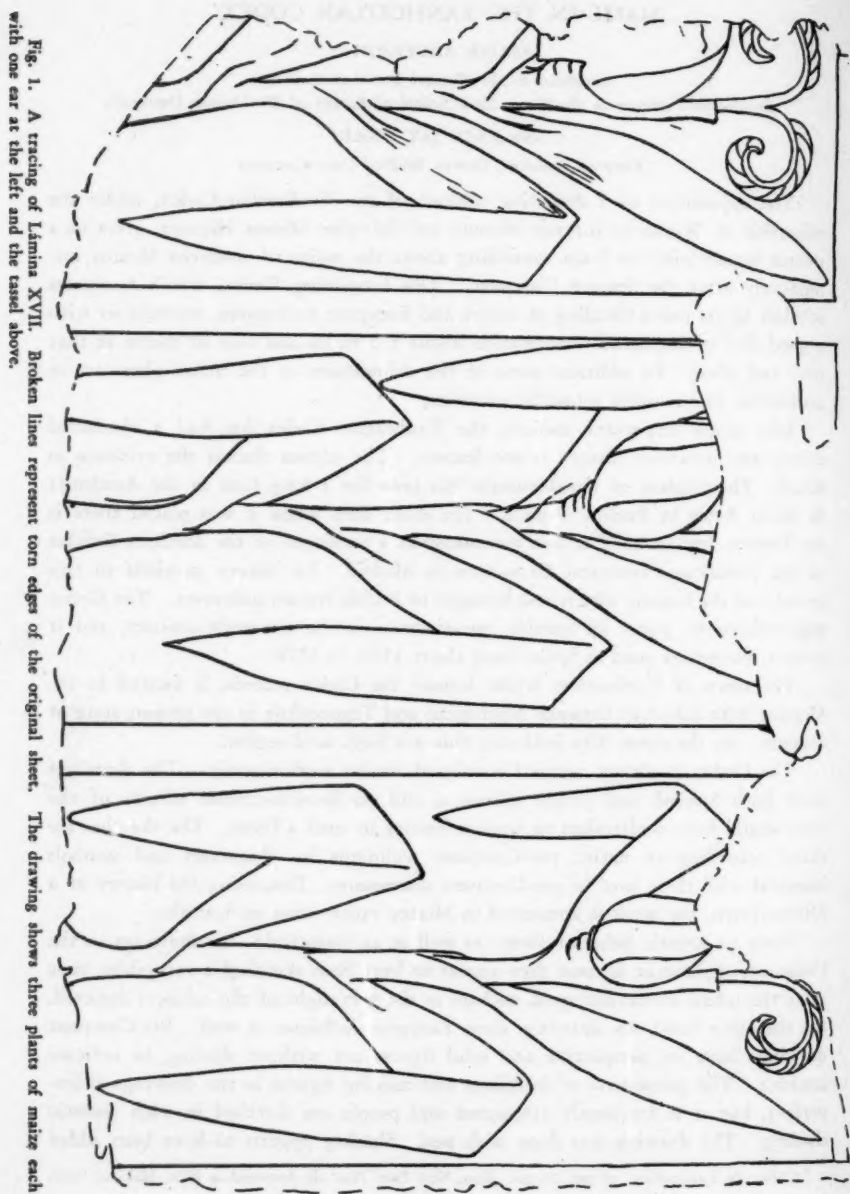
Like many important codices, the Yanhuítlan Codex has had a checkered career, and its entire history is not known. The editors discuss the evidence in detail. The original of the document has been for a long time in the Academia de Bellas Artes in Puebla, Mexico. The exact date when it was placed there is not known, but in 1892 it was mentioned in a catalogue of the Mexican Exhibit of the American Historical Exposition in Madrid. Its history previous to this period and the reasons why it was brought to Puebla remain unknown. The Codex was written on paper of Spanish manufacture in the sixteenth century, and it bears a watermark used in Spain from about 1550 to 1570.

The town of Yanhuítlan, whose history the Codex records, is located in the Mixteca Alta half-way between Nochistlán and Tepozcolula in the present state of Oaxaca. As the name Alta indicates, this is a high, cold region.

The Codex is almost unquestionably of native workmanship. The drawings show both Spanish and Indian influence, and no Spanish-trained scholar of the time would have undertaken to write a history in such a form. The sketches are dated according to native pre-Conquest technique by characters and symbols identical with those used in pre-Conquest documents. Discussing the history of a Mixtec town, the work is annotated in Mixtec rather than in Spanish.

From an artistic point of view (as well as an historical), the drawings in the Codex are significant because they appear to have been sketched a very short time after the actual events occurred, perhaps in the very sight of the subjects depicted. On the other hand, the drawings show European influence as well. Pre-Conquest drawings have no perspective and solid figures are without shading to indicate contour. The perspective of buildings and moving figures in the drawings is imperfect, but it is frequently attempted and people are sketched in with realistic shading. The drawing was done with pen. Shading appears to have been added

<sup>1</sup> *Códice de Yanhuítlan*. 89 pp. 24 pls. Mus. Nac. Inst. Nac. de Antropol. e Hist. Mexico, 1940.



with *píncel* (artist's brush), and this process—used by the aborigines—leads one to believe that the author of the record was already a *tlacuilo* (Aztec scribe) at the time when Spanish culture arrived.

The realism of the drawings demonstrates fairly accurately what kind of maize was under observation by the artist. Mexico now has strikingly different types of maize in different parts of the country. Eventually from archaeological and historical evidence it should be possible to work out in considerable detail the history and origin of the different types as is already being done in other areas.<sup>2</sup>

The maize plants in this figure (pl. 16 and text-fig. 1) are distinguished by their broad, more or less bent leaves, by the short ears whose husks spring out sharply from the stem at almost a right angle, and by coarse tassels with few branches. All these features are characteristic of one of the commonest types of Mexican maize, the many-rowed, short-eared, dent-kernelled varieties which are centered on the region around Mexico City and which Anderson and Cutler<sup>3</sup> have provisionally named "Mexican Pyramidal." The semi-stylized drawings of the

tassel have undoubtedly been influenced by the customary pre-Conquest glyph for the maize plant (a tracing is shown in fig. 2) and therefore may not be too diagnostic. The realistic treatment of the rest of the plant is, however, completely unlike anything in pre-Conquest documents, and is such an exact representation of present-day "Mexican Pyramidal" plants that it presents almost indisputable evidence that the artist had such a plant before him when the drawing was made.

The demonstration that in the late 16th century a Mexican Pyramidal type of maize was being grown in Oaxaca, where such types are to-day exceedingly common, would not be very significant if it were not for an important archaeological fact. The Zapotec funerary

Fig. 2. Pre-Conquest drawing of a maize plant (from the Codex Fejérváry Mayer). Note stylized representation of the three tassel branches. Compare with fig. 1.



urns from near-by regions sometimes include representations of the maize ear in the head-dress of the main figure. These are frequently so stylized as to be useless in determining what type of maize was being grown at the time they were made. A whole group of them, however, are realistic, and many probably represent actual casts made from the ears themselves. Without exception these record a type of maize which is to-day either unknown or at least exceedingly rare in Oaxaca—one which looks different from Mexican Pyramidal varieties

<sup>2</sup> Carter, George F., and Anderson, Edgar. A preliminary survey of maize in the southwestern United States. *Ann. Mo. Bot. Gard.* 32:297-322. 1945.

<sup>3</sup> Anderson, Edgar, and Hugh C. Cutler. *Races of Zea Mays: I. Their recognition and classification.* *Ann. Mo. Bot. Gard.* 29:69-88. 1942.



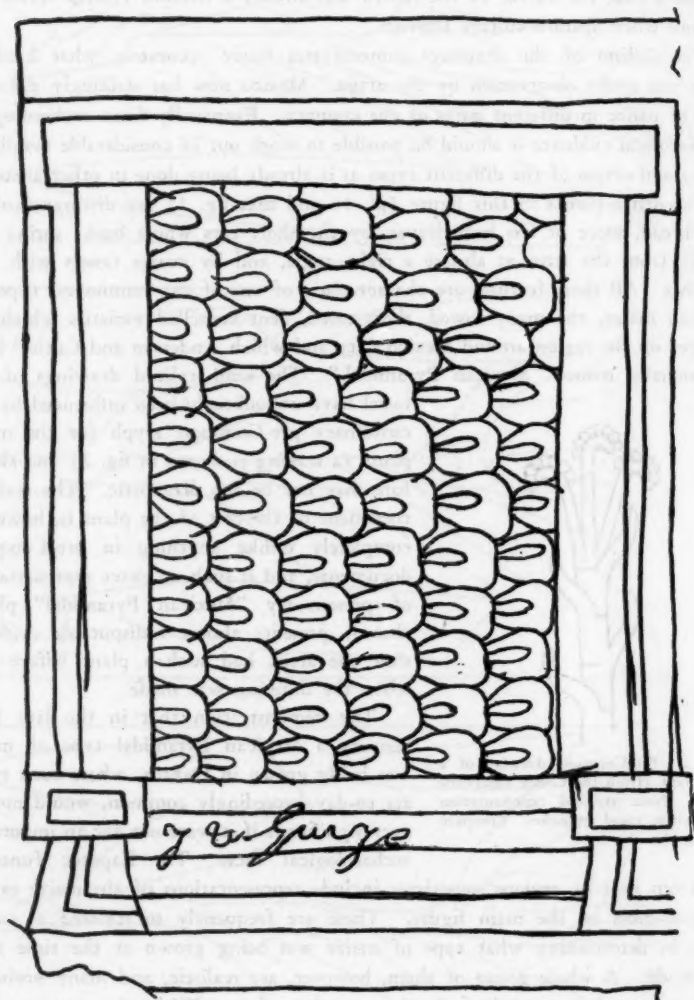


Fig. 3. Tracing of a portion of Lámina XI (see pl. 17) representing a granary filled with maize. The kernels are shown lying on their sides and are obviously derived from the pre-Conquest glyph for maize.



and suspiciously similar to the Basketmaker maize which was being grown in the southeastern United States at about the same period. By analogy with the types of present-day maize which resemble it, we would predict that the maize of the Zapotec funerary urns had narrow tough leaves which did not break readily, that it has long wiry tassel branches with at least 10 to 15 branches in each tassel, and that its husks were wrapped tightly around the ear at the base. Whether or not it was actually of this type, it could not by any stretch of the imagination have been borne on such a plant as the one so realistically depicted in the Yanhuítlán Codex. Such ears could never have been borne in these husks.

The following is a literal translation of the editors' description of the drawings of the maize plant:

Three large rectangular drawings cover this page, but lower and side strokes cannot be seen because the two margins of the paper are lacking. Each of the sketches is a replica drawing of the one and same maize plant. If the plants were drawn with roots, as was the native custom, they cannot be seen because of the frayed margin. The bases of the stalks are broader than other parts, and the plants' corresponding leaves are perfectly drawn, some with their natural creases. An ear of corn covered by its husk is attached to the stalk near the top. The tips of the plant cannot be distinguished because the paper is torn there and the drawings are covered with adhesive tape to hold the page. But in the side sketches parts of the tassels terminating the plant can be seen. It is one of the peculiarities of these drawings that each stalk represents a cornfield during its stage of maturity. It was their custom to express in paintings one single thing to represent the whole.<sup>4</sup>

In addition to defining at least one of the types of maize under cultivation in Oaxaca in the late 16th century, the Yanhuítlán Codex gives us a good deal of incidental information about the culture and uses of maize at that period. The crudely drawn imperial granaries of the pre-Conquest *Matricula*<sup>5</sup> are replaced by more detailed and realistic delineations. The editors describe these drawings as follows:

[The drawings on Lámina XI] represent four granaries drawn like four buildings on platforms, each of which has a high-stoop opposite with four or five treads. Between the lines there is written repeatedly a Mixtec inscription: "*ytū buiyo*" meaning "corn field." [According to the vocabulary of Alvarado, *buiyo* means "corn germinated without sowing it."] On the two sides which define the width of the treads, wooden beams are drawn at the bottom in trapezoidal form, perhaps in order to indicate descent—with parallel lines sketched in as decorations at the edges. These appear to indicate decoratively the formation of ascending and descending steps. And toward the top resting on this section are rectangular roofs somewhat narrower than the parts at the base. In the same direction as these beams, plain window posts arise without other decoration than parallel lines which seem to simulate more elaborately embossed borders. These extend around the lintels resting directly on top of the window posts. As the document lacks colors and these sections do not have description to indicate the material used in its manufacture, it is impossible to determine if the granary is made of wood. But this is probable since it is known that beams were most commonly used in these structures. The roof must have been flat since the top is not drawn otherwise. The interiors of these granaries are full of shelled corn drawn as kernels of large size perfectly recognizable. It should be noted on this page that these four granaries full of corn are the product of four sowings which the Indians of Yanhuítlán are obliged to cultivate in order to satisfy what was prescribed in the required valuation of the governor, Don Domingo, "by reason of its value during the time which he held it." The valuation was made by the Viceroy, Don Antonio de Mendoza, October 26, 1548, and, after estimating

<sup>4</sup> *Op. cit.* Lámina XVII, pp. 64-65.

<sup>5</sup> Anderson, Edgar, and R. H. Barlow. The maize tribute of Moctezuma's empire. *Ann. Mo. Bot. Gard.* 30:413-420. 1943.

other loans, it mentions: "They are to reap four more sowings of corn; two of these have 400 *brazas en quadro* each; the third, 300; and the fourth, 600."<sup>6</sup>

The widespread use of maize as a tax or tribute is referred to in the editors' study of the Codex:

... In order for all the priests of S. Domingo to enjoy the fruition of this cornfield [in Yanhuítlan] ... they will be given the harvests of wheat and corn for the sustenance of all the priests ...<sup>7</sup>

... [The Indians] will make four more plantings of corn, two of which will reap 400 *brazas en quadro*, a third, 300, and the fourth, 600.<sup>8</sup>

... Each of them pays in taxes 782 pesos and half in gold dust, and they plant 15 *banegas* of wheat; ... 700 tortillas of maize and 30 *buesos* and a half *banega* of maize ... This is a fertile land for corn and wheat ...<sup>9</sup>

It is interesting to note from the Codex that maize was carried in packs in exactly the manner which prevails today in parts of Mexico. The authors comment on Lámina XII as follows:

... In the center of the upper half, one sees the picture of a *tameme*, a native carrier whose body is covered by nothing other than a *maxtlatl*, without any decoration. This, together with the duty he is performing, indicates his low condition. One of the ends of the cloth covering him falls to the front, and the other is knotted at the back of the belt then hangs down. The carrier's burden consists of a thinly woven sack full of shelled corn which he carries by using a *mecapal* [tump line, *i.e.* a long rope used by porters with a flat band fitting over the forehead]. This object, still used today, consists of a fiber woven from maguay in the form of a band, and variable in width as much as ten centimeters; on its ends it has some handles made of textile material. Cords are attached to these tying the weight.<sup>10</sup>

<sup>6</sup> *Op. cit.*, Lámina XI, pp. 61-62.

<sup>7</sup> *Op. cit.* p. 33.

<sup>8</sup> *Op. cit.* p. 36.

<sup>9</sup> *Op. cit.* p. 33.

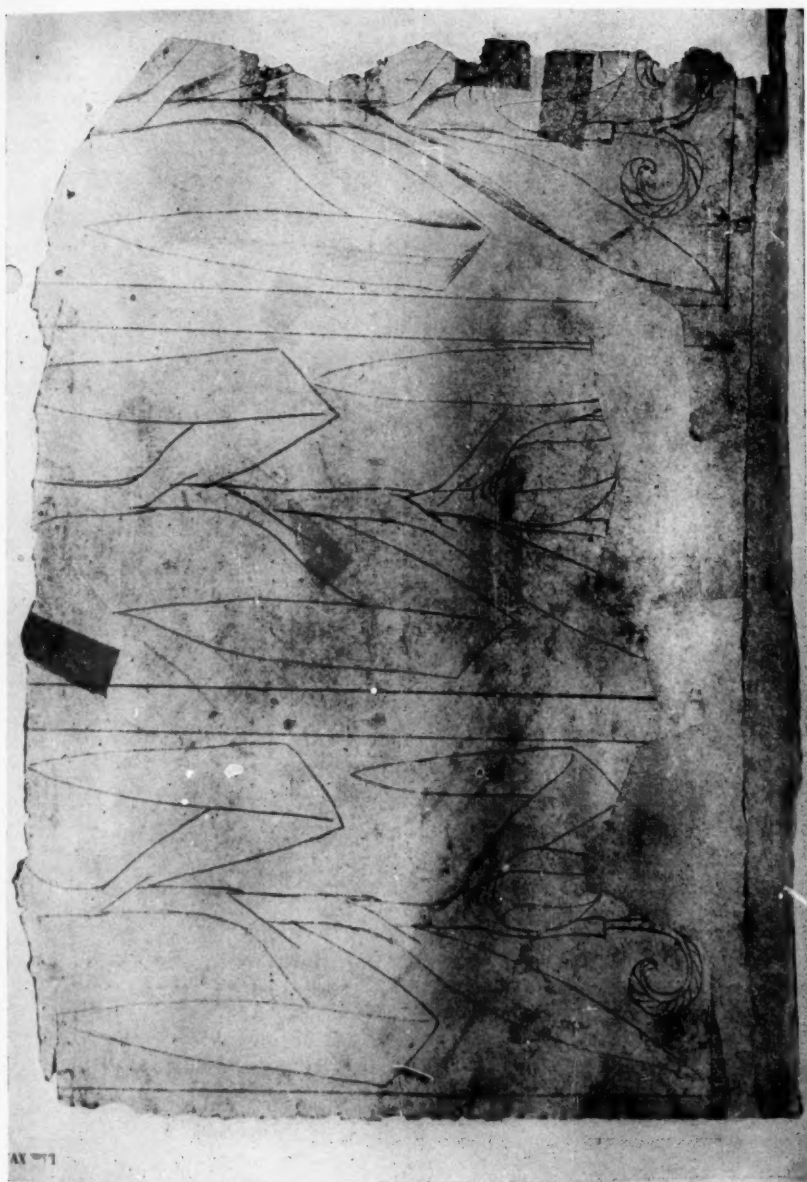
<sup>10</sup> *Op. cit.* p. 61.

#### EXPLANATION OF PLATE

##### PLATE 16

Lámina XVII of the Yanhuítlan Codex, showing three plants of maize, each one of which probably symbolizes an entire field (see text). A tracing of this *lámina* is shown in text-fig. 1.

ANDERSON & FINAN — MAIZE IN THE YANHUITLAN CODEX

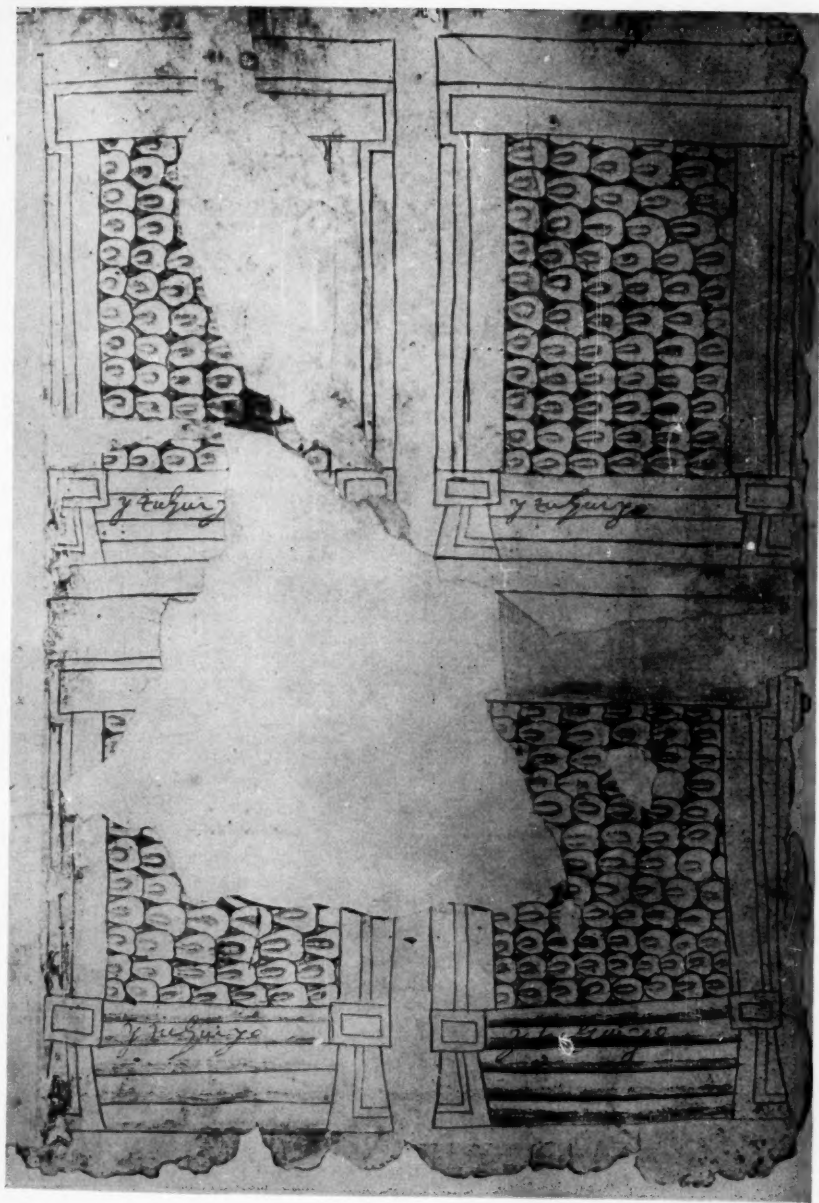


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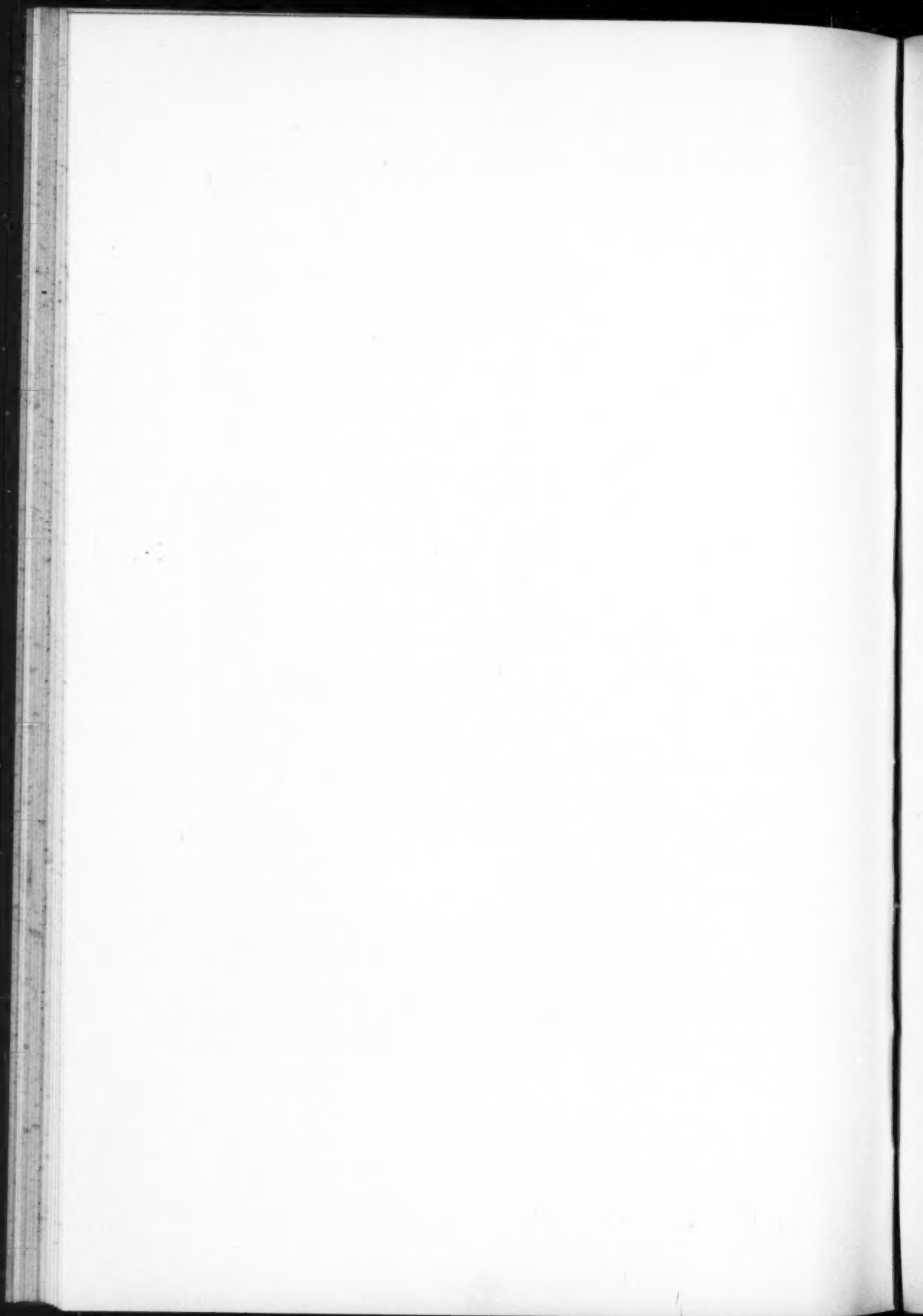
## EXPLANATION OF PLATE

## PLATE 17

Lámina XI of the Yanhuitlán Codex. Four granaries (*trojes*) filled with maize. A tracing of the upper right-corner is shown in text-fig. 3.



ANDERSON & FINAN — MAIZE IN THE YANHUITLAN CODEX





## NOTES ON SOME NORTH AMERICAN ASCLEPIADS<sup>1</sup>

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### ASCLEPIODORA DECUMBENS WHEN TREATED AS AN ASCLEPIAS

The first results of my studies of the American Asclepiads were embodied in a "perspective" of the genera (Ann. Missouri Bot. Gard. 28:193-244. 1941), prominent within which was a drastic reduction of the segregate genera *Acerates*, *Asclepiodora*, *Solanoa*, *Podostigma*, and many others, to *Asclepias* L. That treatment was intended as a reformation of the generic lines, and although numerous illustrative changes of nomenclature were introduced, keys to all the included species, and their synonymy, were not provided. As I pointed out at the time, appropriate combinations under *Asclepias* already were available, with relatively few exceptions, some of which were offered thereupon. One case which I neglected, however, was that of the familiar "Antelope-horns" of the southwestern States, *Asclepiodora decumbens* (Nutt.) A. Gray. In the interval since the 1941 publication, I have received a number of requests for the correct name of this plant when considered under *Asclepias*, from botanists who are aware of the earlier homonym *A. decumbens* L.

At first glance, an early name for *Asclepiodora decumbens* seems to be provided in *Asclepias brevicornu* Scheele (Linnaea 21:756. 1848) as indicated arbitrarily by 'Index Kewensis', but further consideration shows that this disposition probably is incorrect. The description of Scheele's plant, *Römer s. n.* from the neighborhood of New Braunfels, Texas, paradoxically points to synonymy with the fortunately earlier *A. longicornu* Benth., which is common in the same vicinity. Association of *A. brevicornu* with *A. longicornu* is suggested strongly by the following excerpts from the original diagnosis of the former: "*Corolla . . . lacinae . . . primo patulae, dein reflexae. Corona . . . cuculli speciosi aurantiaci falcati oblongo apice rotundati medio utrinque auriculati processum brevissimum includentes gynostegio longiores . . .*" Scheele further remarks concerning the chief distinguishing characters of his species: "Eine prachtige, durch das sehr kurze Horn und die schönen, sichelförmigen, beiderseits geörhten Klappen ausgezeichnete Art, mit Keiner andern zu verwechseln!" It is obvious, at least, that Scheele did not consider his *A. brevicornu*, indicated by 'Index Kewensis' as a synonym of *Asclepiodora decumbens*, as at all closely related to the next species that he proceeded to describe, *A. longipetala*, based upon a Lindheimer collection from New Braunfels fortunately available in the herbarium of the Missouri Botanical Garden. This happens to be the common plant known as *Asclepiodora viridis*

<sup>1</sup>Continued from Ann. Missouri Bot. Gard. 31:369. 1944.  
Issued September 15, 1945.

(Walt.) A. Gray (*Asclepias viridis* Walt.), which anyone will grant to be extremely closely related, indeed, to *Asclepiodora decumbens*.

An examination of the diagnosis of *Asclepias brevicornu* shows further the impossibility of classifying it as an *Asclepiodora*, particularly in the characters of the reflexed corolla and the "schönen, sichelförmigen, beiderseits geörhten Klappen [hoods]." These immediately place the plant as a member of Kunth's old genus *Otaria*, exemplified by such species as *A. longicornu*, *A. nyctaginifolia*, *A. Emoryi*, and *A. subulata*. Only the first of these could have been collected in the vicinity of New Braunfels, with the possible exception of *A. Emoryi*, the hoods of which are too short to coincide with Scheele's diagnosis. The discrepancy of Bentham's and Scheele's names apparently for the same species is explained by the allusion of the former to the strikingly elongate hoods and of the latter to the short, adnate horns.

Since *Asclepias brevicornu* Scheele is not available as a name for *Asclepiodora decumbens* when treated as an *Asclepias*, and since none other exists, it becomes necessary to coin a new name (in allusion to the popular name):

**ASCLEPIAS capricornu** Woodson, nom. nov.

*Anantherix angustifolia* Raf. Atl. Journ. 146. 1832, non *Asclepias angustifolia* Schweig.

*Anantherix decumbens* Nutt. in Trans. Amer. Phil. Soc. 5:203. 1837, non *Asclepias decumbens* L.

*Anantherix Nuttalliana* G. Don, Gen. Hist. 4:146. 1838, nec *Asclepias Nuttalliana* Tor., nec A. Gray.

*Acerates decumbens* (Nutt.) Dcne. in DC. Prodr. 8:522. 1844.

*Asclepiodora decumbens* (Nutt.) A. Gray, in Proc. Amer. Acad. 12:67. 1876.

*Asclepias decumbens* (Nutt.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>:239. 1895, non L.

*Asclepias capricornu* occupies a wide territory of the southwestern United States from central Kansas to east-central Texas and westward to Arizona and southern Nevada. Over this area it is not a phenotypic unit. Preliminary studies have satisfied me of the presence of well-defined continuous obliquely stepped clines (J. S. Huxley, in Bijdr. Dierk. 27<sup>2</sup>:494. 1939) of an east-west direction in at least four essential characters of the plants. These are found in the leaf base, presence or absence of a naked peduncle, hood color, and follicle surface. Unfortunately, three of these are essentially qualitative in nature. However, when assigned arbitrary scores and plotted, a biologically significant discontinuity is discovered for all four characters centering in western Texas. In the zone of intergradation, the cline is conspicuously steep, and, as I have said, occurs at almost the same gradient for all four characters.

Such being the case, it appears appropriate to indicate two subspecies: an eastern (including the typical element of the species) characterized by obtuse leaf bases, sessile inflorescences (i. e., immediately subtended by leaves), light-colored hoods, and more or less spiny follicles, and a western, characterized by narrowly acute leaf bases, pedunculate inflorescences, dark-colored hoods, and

smooth follicles. I expect to investigate the relationship of these subspecies more fully when conditions permit.

*ASCLEPIAS CAPRICORNU* ssp. **capricornu** Woodson, ssp. nov.

Speciei elementum typicum; foliis basi vulgo obtusis nisi truncatis; inflorescentiis sessilibus vel subsessilibus; coronae cucullis vulgo pallidis; folliculis plus minusve spinosis.

*ASCLEPIAS CAPRICORNU* ssp. **occidentalis** Woodson, ssp. nov.

Plantae speciei habitu congruentes sed foliis angustioribus basi plerisque anguste acutis; inflorescentiis plus minusve valde pedunculatis; coronae cucullis plus minusve saturate purpureis; folliculis laevibus.—Exemplum typicum: NEVADA: CLARK: Pine Canyon. Roadside near stream. With *Juniperus utabensis* and *Pinus monophylla*. Alt. 1800 m. May 24, 1940. I. W. Clokey 8613 (Herb. Missouri Bot. Gard., **TYPUS**).

(To be continued)



